ANNUAL REVIEWS

Annual Review of Ecology, Evolution, and Systematics

Observed and Potential Range Shifts of Native and Nonnative Species with Climate Change

Bethany A. Bradley,[1,2] Evelyn M. Beaury,[3]
Belinda Gallardo,[4] Inés Ibáñez,[5] Catherine Jarnevich,[6]
Toni Lyn Morelli,[2,7] Helen R. Sofaer,[8]
Cascade J.B. Sorte,[9] and Montserrat Vilà[10,11]

[1]Department of Environmental Conservation, University of Massachusetts, Amherst, Massachusetts, USA; email: bbradley@eco.umass.edu

[2]Northeast Climate Adaptation Science Center, University of Massachusetts, Amherst, Massachusetts, USA

[3]Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey, USA

[4]Instituto Pirenaico de Ecología, Consejo Superior de Investigaciones Científicas, Zaragoza, Spain

[5]School for Environment and Sustainability, University of Michigan, Ann Arbor, Michigan, USA

[6]US Geological Survey, Fort Collins Science Center, Fort Collins, Colorado, USA

[7]US Geological Survey, Northeast Climate Adaptation Science Center, Amherst, Massachusetts, USA

[8]US Geological Survey, Pacific Island Ecosystems Research Center, Hawaii National Park, Hawaii, USA

[9]Department of Ecology and Evolutionary Biology, University of California, Irvine, California, USA

[10]Doñana Biological Station, Spanish National Research Council (EBD-CSIC), Sevilla, Spain

[11]Department of Plant Biology and Ecology, University of Sevilla, Sevilla, Spain

Annu. Rev. Ecol. Evol. Syst. 2024. 55:23–40

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

https://doi.org/10.1146/annurev-ecolsys-102722-013135

Keywords

alien species, biological invasion, global environmental change, range shift, species spread rate, species distribution modeling

Abstract

There is broad concern that the range shifts of global flora and fauna will not keep up with climate change, increasing the likelihood of population declines and extinctions. Many populations of nonnative species already have advantages over native species, including widespread human-aided dispersal and release from natural enemies. But do nonnative species also have an advantage with climate change? Here, we review observed and potential range shifts for native and nonnative species globally. We show that nonnative species are expanding their ranges 100 times faster than native species, reflecting both traits that enable rapid spread and ongoing human-mediated introduction. We further show that nonnative species have large potential ranges and range expansions with climate change, likely due to a combination of widespread introduction and broader climatic tolerances. With faster spread rates and larger potential to persist or expand, nonnative populations have a decided advantage in a changing climate.

1. INTRODUCTION

Conservation scientists worry that native flora and fauna will not shift their ranges quickly enough to keep up with rapid climate change (IPCC 2023), leading to large-scale population declines and alterations to the composition and diversity of ecological communities (e.g., Chen et al. 2011, Lenoir & Svenning 2015, Pecl et al. 2017). At the same time, invasion scientists worry that nonnative flora and fauna could expand rapidly into new regions (e.g., Dukes & Mooney 1999, Hellmann et al. 2008), further exacerbating their ecological impacts. This juxtaposition seems to present a conflict. Native species, which inhabit their historical geographic range, are expected to fail to expand while nonnative species, which inhabit a novel geographic range due to human introduction, are expected to succeed. Here, we review the evidence associated with these two expectations to ask: Does climate change create an advantage for nonnative species?

Native species: populations of species within the limits of their historical natural range

Nonnative species: species with established populations (i.e., viable self-sustaining populations) outside of their historical range due to either accidental or intentional human transportation and introduction; also termed alien, displaced, exotic, introduced, or nonindigenous

Niche: the combination of biotic and abiotic conditions in which a species can maintain a population (i.e., fundamental niche); observations of species typically capture a portion of its niche (i.e., realized niche) because species have not dispersed into all available habitat and some suitable environmental conditions may not exist

For populations to persist with climate change, both native and nonnative species have to adapt in place and/or shift their geographic ranges to maintain their ecological niches (Davis & Shaw 2001, Hutchinson 1957). Climatic tolerance is an important determinant of a species' niche because most species are limited in some way by temperature or precipitation (e.g., Pearson & Dawson 2003, Whittaker 1970). While species' ecological niches may change over time due to adaptation (Somero 2010), species ranges are likely to change much more rapidly (e.g., Quintero & Wiens 2013, Willis & MacDonald 2011). With temperatures warming across the planet (IPCC 2023), species ranges are generally projected to shift to higher latitudes (poleward), higher elevations (upward), and/or deeper depths. However, there is large variation among species in terms of whether ranges are projected to expand, remain stable, or contract with climate change (e.g., Warren et al. 2018).

Although species ranges have always shifted in response to climate (e.g., Jackson et al. 1997, Willis & MacDonald 2011), current rates of climate change are orders of magnitude faster than those that species have experienced during their evolutionary history (IPCC 2023, Williams et al. 2007). The current velocity of climate change, or the rate of geographic shift required for species to track rising temperatures (Loarie et al. 2009), has been estimated to average 3.25 km/year on land (Dobrowski & Parks 2016) and 2.75 km/year in the ocean (Burrows et al. 2011). Climate velocities are even higher in areas warming at faster rates [e.g., at higher latitudes (Burrows et al. 2011)] and where species need to move around barriers to dispersal [e.g., in patchy habitats or complex topography (Dobrowski & Parks 2016)]. Rapid warming will require species to shift their ranges at unprecedented rates to keep up with climate change.

Given that all species need to shift their ranges to keep up with climate change, species origin (native versus nonnative) may seem like an arbitrary distinction. However, considering origin is important because it may affect not only the ability of species to keep up with climate change but also their role in an ecosystem. First, nonnative species rarely provide equivalent ecosystem benefits to those provided by native species, generally supporting less diverse ecosystems. For example, nonnative plants host an average of 14 times fewer species of native *Lepidoptera* than native plants

(Tallamy & Shropshire 2009). Similarly, nonnative tree plantations contain few native plants while adjacent native forests contain predominantly native understory plants, including species of conservation concern (Vu Ho et al. 2023). Indeed, nonnative species are associated with biotic homogenization, where the combination of loss of rare species and addition of the same nonnative species creates an ecological sameness of flora and fauna across landscapes (Petsch et al. 2022).

Second, nonnative species have the potential to become invasive. Invasive species are a subset of nonnative species whose populations are spreading within their nonnative range and have detrimental impacts on biodiversity, ecosystems, and ecosystem services (Roy et al. 2023). Over 30% of nonnative vertebrate and invertebrate species and over 20% of nonnative plants may become invasive and ecologically harmful globally (Jeschke & Pyšek 2018, Pfadenhauer & Bradley 2024). Invasive species harm ecosystems by consuming native flora and fauna (e.g., Gallardo et al. 2016); outcompeting native species for resources like nutrients, shelter, and space (e.g., Liebhold et al. 2017); and even altering ecosystem structure and function (Roy et al. 2023). Collectively, invasions lead to declines in native populations and diversity (Bradley et al. 2019) and can drive native species to local extinction (Bellard et al. 2016). These clear differences in the ecological benefits and in the potential for ecological harm between native and nonnative species make it important to consider how species origin interacts with climate change.

Moreover, with widespread and increasing introductions of nonnative species into new regions or countries (hereafter, human-mediated introductions) (Seebens et al. 2017), there is reason to believe that nonnative species have an advantage in keeping up with climate change. Many nonnative species are intentionally introduced, for example, via the pet, aquarium, and ornamental plant trades, and become established following accidental escape into natural areas (Lockwood et al. 2019, Padilla & Williams 2004, Reichard & White 2001). Global trade also creates numerous accidental introductions, with nonnative species transported either as contaminants of a commodity or as stowaways in traded goods (Hulme et al. 2008). Human activities not only introduce nonnative species to new areas but also often continue to facilitate dispersal once species are introduced, both intentionally [e.g., in home and urban gardens (Bayón & Vilà 2019, Beaury et al. 2021)] and accidentally [e.g., by ballast water or through marine corridors (Rilov & Galil 2009)].

Although the human-mediated introduction of nonnative species over long distances and outside their native ranges is common, the introduction of native species to expand their historical native range in response to climate change remains relatively rare (e.g., Breed et al. 2018). Instead, human-mediated introduction of native species typically focuses on reintroducing species in areas where they have gone locally extinct, increasing the populations of native species of conservation concern, supporting commercial or recreational stocks, or restoring habitats. Native species that have shifted their ranges outside of their historical native range (e.g., in response to climate change) are termed neonative (Essl et al. 2019), and there is ongoing debate as to whether range-shifting native species are a cause for concern versus a beneficial phenomenon that should be encouraged (Nackley et al. 2017, Wallingford et al. 2020). Of even greater debate in conservation and management is the idea of assisted migration, or the intentional introduction of native species outside of their native range and into habitats becoming newly suitable due to climate change (McLachlan et al. 2007). For example, only in 2023 did United States' federal government policy generally allow for the assisted migration of rare and endangered species to enable range shifts of species at risk of extinction in their historical range (USFWS 2023).

Although science and management approaches to native and nonnative species differ, the two sets of species are affected by similar climate-driven forces. First, many studies have already observed species shifting their ranges in response to climate change (e.g., Lenoir et al. 2020, Parmesan & Yohe 2003), but rates of spread and ability to keep up may differ between native and nonnative species (Sorte et al. 2010). Second, projections of species' distributions with climate

Species range: geographical area of a species occurrence

Velocity of climate change: rate of movement along the Earth's surface required to maintain a constant temperature

Dispersal: movement of a species within or beyond its native or nonnative range where it might establish a new population

Invasive species: subset of nonnative species that have established populations that are spreading within the introduced range and have a negative impact on biodiversity, local ecosystems, species, or ecosystem services

Spread: the movement of a species within or beyond its native or nonnative range and subsequent establishment of a population change indicate that the ranges of both groups are likely to shift (e.g., Pearson & Dawson 2003), but the area of potential range expansion and range contraction may also differ between native and nonnative species. Here, we review studies of observed and potential range shifts for native and nonnative species to uncover any differences between the two groups and address whether climate change is likely to create an advantage for nonnative species.

Human-mediated introduction: intentional or unintentional introduction of nonnative species into a new region; there are six principal introduction pathways: release (e.g., game animals), escape (e.g., spread from gardens), contaminant (e.g., insect on nursery plant), stowaway (e.g., larvae in ballast water), corridor (e.g., interconnected waterways), and unaided (i.e., natural dispersal across political borders)

Neonative: populations of species that have expanded the limits of their historical natural range in response to human-caused environmental change

Assisted migration: the intentional human-mediated movement of a species into habitats anticipated to be suitable due to climate change

Range shift: directional change in a species' geographic distribution, for example, in response to climate change

2. OBSERVED MOVEMENT: HOW FAST ARE NATIVE SPECIES SPREADING IN COMPARISON TO NONNATIVE SPECIES?

In order to assess how well native versus nonnative species might keep up with climate change, we compiled observations of species spread rates across different taxa and ecosystems. In recent decades, there has been a strong scientific focus on testing whether native species ranges are shifting in response to climate change (e.g., Lenoir et al. 2020, Parmesan & Yohe 2003, Rubenstein et al. 2024). Analyses of whether nonnative species are shifting in response to climate change are less common because many are actively expanding in all directions due to a lack of equilibrium with the environment of their introduced range (Václavík & Meentemeyer 2012). Thus, it is likely that natural dispersal and human-mediated secondary spread, rather than climate change, are the main drivers of existing observations of nonnative species' movement.

Nevertheless, nonnative species spread rates have been measured at two distinct spatial scales. First, at larger spatial scales, human-mediated introductions can be used to estimate spread rate directly associated with humans (Seebens et al. 2021). Although not classically thought of as spread, human-mediated introductions continue to facilitate the secondary spread of nonnative species within their nonnative ranges (e.g., Beaury et al. 2021) and are therefore important to consider. Second, at finer spatial scales, numerous studies have measured the secondary spread of nonnative species following their introduction into a novel geographic range (e.g., Horvitz et al. 2017, Rapoport 2000). These measures of secondary spread typically aim to measure natural dispersal but may include a combination of natural dispersal and human-mediated secondary spread.

We compared three observed rates of spread: native species spread, nonnative species secondary spread, and human-mediated introductions of nonnative species. We expected that rates of native species spread would be lower than rates of nonnative species secondary spread, which would be lower than rates of human-mediated introductions.

For native species, we compiled data on observed range shifts as a measure of native species spread using a database derived from a systematic literature review by Rubenstein et al. (2024) (**Supplemental Appendix 1**), which is a comprehensive compilation of observational studies of species range shifts in response to current climate change. From this database, we included only studies that examined leading edge spread rates and showed a positive or no change in species range; we excluded those showing a range contraction, as equivalent data for nonnative species are lacking. Where there were multiple observations across studies or locations for a single species, we averaged the spread rates.

For nonnative species, we compiled data on rates of secondary spread using previous reviews (Rapoport 2000, Vilà et al. 2021) and literature searches on Web of Science (**https://webofknowledge.com**) (**Supplemental Appendix 1**). Although methods vary by study, rates are typically based on changes in the observed distribution of nonnative species across consecutive surveys or on the maximum observed distance of secondary spread from the initial introduction location after a particular time. If several spread rates were given for the same species at a single location for different periods of time, we recorded the average spread rate. If spread rates were given for multiple locations, within or across studies, we recorded all spread rates and then calculated an average spread rate for each species.

For human-mediated introductions of nonnative species, we obtained data from Seebens et al. (2021). Using these data, we calculated the average distance between a new record of a nonnative species and each previous record using the Alien Species First Record Database (Seebens et al. 2017). The data are reported at the country scale, and rates are based on average distance divided by time between records. Because the introduction rates change over time (newer records are closer together as a species is introduced to more countries), we selected only species with records in more than 20 regions and averaged the rates by species.

In our comparison, we included species in taxonomic classes that had at least two measurements for native spread, nonnative secondary spread, or human-mediated introduction rates, resulting in measurements from 249 native species, 242 nonnative spreading species, and 192 nonnative species with human-mediated introductions. Classes included mammals (Mammalia), birds (Aves), ray-finned fishes (Actinopterygii), insects (Insecta), crustaceans (Malacostraca), gastropods (Gastropoda), dicot flowering plants (Magnoliopsida), and monocot flowering plants (Liliopsida). To avoid overrepresenting classes with more species (**Supplemental Appendix 1**, **Supplemental Table 1**), we randomly selected a comparable number of species for each of the three groups (native spread, nonnative spread, and human-mediated introduction) to calculate average spread rates.

Human-mediated introductions were significantly faster than nonnative spread, and both were significantly faster than native spread (Kruskal–Wallis test, $X^2 = 535$, degrees of freedom $= 2$, $p < 0.001$) (**Figure 1*a***). The average spread rate (mean ± SD) associated with human-mediated introductions of nonnative species (1,883 ± 434 km/year) was more than 50 times faster than nonnative species secondary spread (35 ± 67 km/year) and 1,000 times faster than the average rate of native species spread (1.74 ± 4.11 km/year). Similarly, the average nonnative species secondary spread rate was over 20 times faster than the average rate of native species spread (**Supplemental Appendix 1**, **Supplemental Table 1**).

Within taxonomic groups, the biggest differences were found for dicot flowering plants, where spread rates (mean ± SD) for human-mediated introduction (1,911 ± 486 km/year) and nonnative

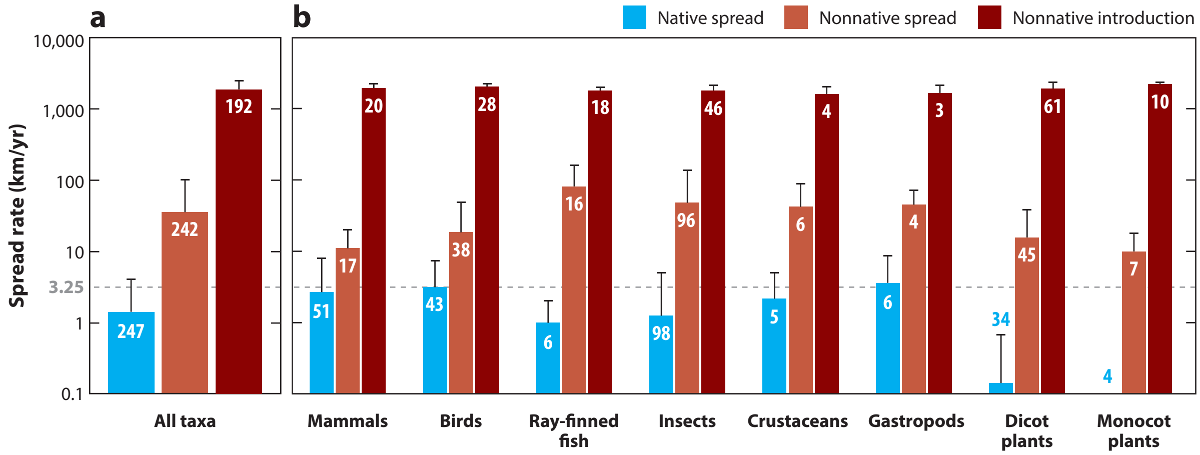

Figure 1

Observed spread rates between native and nonnative species (*a*) across and (*b*) within taxonomic classes. The average rates of native species' spread (*blue*), nonnative species' secondary spread within the introduced range (*light red*), and nonnative species' spread rates due to human-mediated introduction (nonnative introduction; *dark red*) across all taxa. Differences in spread rates for the three groups are highly significant across and within taxa ($p < 0.001$) (**Supplemental Table 1**). Error bars represent the standard deviation. Numbers indicate the sample size (*n* species). The gray dashed line represents the average velocity that terrestrial species need to move to keep up with climate change (3.25 km/year). Note that the data are presented on a log scale.

Historical range: native geographic area of a species reflecting its environmental limitations, evolutionary history, and dispersal capacity

Range expansion: establishment of a species in areas beyond its historical range, e.g., in response to climate change

Range contraction: disappearance of a species from part of its historical range, e.g., in response to climate change species secondary spread (15.5 ± 23.0 km/year) were 14,000 and 100 times faster, respectively, than that of native species (0.14 ± 0.54 km/year) (**Figure 1*b***). Similarly, nonnative ray-finned fish (1,800 and 80 times faster for human-mediated and nonnative spread, respectively) and insects (1,200 and 30 times faster for human-mediated and nonnative spread, respectively) spread at substantially higher rates than their native counterparts (**Supplemental Appendix 1**, **Supplemental Table 1**). Although mobile species such as vertebrate and invertebrate animals might be expected to move faster than sessile species (i.e., plants), there were no significant differences (post-hoc Tukey test, $p > 0.05$) (**Figure 1*b***; **Supplemental Appendix 1**, **Supplemental Table 2**) with two exceptions: The secondary spread of nonnative ray-finned fish was higher than those of nonnative dicot flowering plants (Tukey test, $p = 0.02$) and birds (Tukey test, $p = 0.06$), and the spread rates of native birds were higher than those of native dicot flowering plants (Tukey test, $p = 0.04$).

Secondary spread: dispersal of a nonnative species after its initial human-mediated introduction; secondary spread could be biological, human-mediated, or both

Trait: morphological and functional characteristic of a species including those related to physiology, biomass allocation, growth rate, size, and fitness

3. WHY ARE NONNATIVE SPECIES SPREADING FASTER?

Observations of native and nonnative species' spread rates (**Figure 1**) clearly illustrate that nonnative species, spreading within their nonnative range at an average rate of 35 km/year, are well poised to keep up with the velocity of climate change (2.75 km/year in the ocean; 3.25 km/year on land). In contrast, many native species, calculated here to be spreading at an average rate of 1.74 km/year, may fall behind. Moreover, our calculated native species spread rate is likely an overestimate of overall spread given that we focused only on positive measures of expansion at the leading edge to be more comparable to nonnative species spread measurements. A recent paper that included zeroes and negative values calculated the average native species spread rate to be 1.11 km/year (Lenoir et al. 2020). This disconnect between spread rates and the velocity of climate change is particularly acute for native plants, which are moving an order of magnitude slower (0.14 km/year) on average. The faster spread rates of nonnative species may be due to human selection of species with traits that lead to faster dispersal, ecological and evolutionary advantages that species gain in their nonnative range, and/or continued association with and assistance from humans both within and across regions.

3.1. Nonnative Species' Traits Confer an Advantage

Rapid growth rates, prolific reproduction, generalist behavior, and phenotypic plasticity are all common traits among nonnative species that not only contribute to their ability to establish successfully in a new range (van Kleunen et al. 2018a) but also support the rapid spread rates needed to track a changing climate (Simberloff 2000). Population spread is highly dependent on reproductive output (Clark et al. 2001), which contributes to a higher incidence of long-distance dispersal events (Clark et al. 1999) and to faster population growth once established (Capellini et al. 2015). For example, using a meta-analysis, Mason et al. (2008) found that nonnative invasive plants had higher fecundity than cooccurring native species, producing 6.7 times more seeds and increasing their potential for population spread. Likewise, fast population growth and high competitive performance, common among invasive species, contribute to faster nonnative plant spread by increasing the availability of propagules (Ibáñez et al. 2009). Additionally, nonnative animals tend to be less sensitive than their native counterparts to extreme weather events like heat waves, cold spells, storms, and floods, whose frequency is expected to increase under climate change scenarios (IPCC 2023, Gu et al. 2023), and nonnative plants tend to be favored with climate change due to their tendency to respond to temperature rather than daylight cues (Willis et al. 2010). All of these traits may contribute to faster spread rates of nonnative species under climate change.

Individual populations of nonnative species may also have higher fitness and greater ability to spread than native populations due to high genetic diversity. Nonnative populations have historically been viewed as experiencing genetic bottlenecks that might limit population establishment (for examples, see Hänfling 2007). However, studies from disparate taxa using molecular markers now show that multiple independent introductions from a variety of sources across the native range are typical for nonnative species introduction. This phenomenon leads to substantial genetic variation among nonnative populations, with genes drawn from multiple geographically distinct populations from the native range (e.g., Castagné et al. 2023, Smith et al. 2020). Genetic variation through admixture of multiple population sources might enhance rapid adaptation to new environmental conditions (Kolbe et al. 2007) and aid in population range expansion (Rius & Darling 2014) due to the presence of individuals with traits that support faster spread.

The transport and introduction of nonnative species is also likely to select for traits that support rapid spread and enable population growth (Colautti et al. 2006, Theoharides & Dukes 2007). For example, rapid growth rates are a desirable trait in ornamental plants (van Kleunen et al. 2018b), which is the primary pathway of nonnative plant introductions (Reichard & White 2001). Nonnative species might also be better equipped to spread due to fewer predators and herbivores keeping them in check. In the native range, coevolved natural enemies can constrain species' population growth and subsequent spread (Maron & Vilà 2001), but many studies show that nonnative plants released from above- and belowground herbivores and pathogens invest more resources in growth and reproduction than native plants (Liu & Stiling 2006, Zhao et al. 2020). Although studies quantifying how the lack of natural enemies translates to plant population dynamics are scarce, it is plausible that enemy release enables nonnative species to become more abundant and spread faster into new habitats (DeWalt et al. 2004). The bulk of evidence for the population benefits of enemy release has been found in plants, but studies have also demonstrated release from pathogens and parasites and associated demographic advantages in nonnative animals (Torchin & Mitchell 2004), indicating that enemy release could support faster nonnative spread across taxa.

Enemy release: decrease in the population regulation of introduced nonnative species into a new region by herbivores, parasites, and pathogens, resulting in a rapid increase in their abundance

3.2. Nonnative Species' Introduction Patterns Confer an Advantage

In addition to differences in traits that affect spread rates, there are substantial differences in geography between native and nonnative species. Specifically, the availability and accessibility of unoccupied habitat that a species could potentially spread into differs systematically between native and nonnative populations (González-Moreno et al. 2015). For native species, habitat that becomes newly suitable under climate change typically emerges at one edge of the range—poleward or toward higher elevations (Lenoir et al. 2020, Mason et al. 2015) (**Figure 2*a***). Due to suboptimal environmental conditions, native species tend to exhibit diminished reproductive outputs at the edges of their climatic range (e.g., Kawecki 2008), which likely reduces reproductive performance and spread rates. Additionally, directional dispersal in response to climate change may be limited by natural and human-created dispersal barriers (Dobrowski & Parks 2016), slowing or halting native species' spread rates. In contrast, nonnative species are less likely to have established throughout all available habitat (Bradley et al. 2015, González-Moreno et al. 2015), creating opportunities to spread from multiple introduction points and in multiple directions (**Figure 2*b***). Similarly, unintentional introductions of species such as nonnative invertebrates via contaminant or stowaway pathways can lead to spread from multiple points of introduction (e.g., Jacobi et al. 2012), resulting in high rates of secondary spread. Thus, nonnative species might have higher observed spread rates (**Figure 1**) because having multiple introduction sites allows them to overcome dispersal barriers.

In addition to having fewer limits on spread direction, nonnative species often have an advantage due to close association with humans; indeed, many have been introduced because of their utility to humans. Rather than limiting habitat connectivity, human land uses can create corridors for rapid dispersal of nonnative species (Resasco et al. 2014), while disturbance can

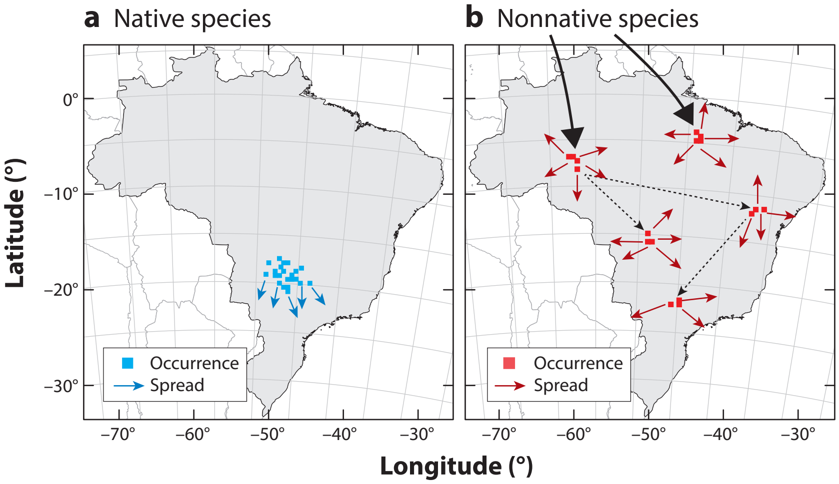

Figure 2

Occurrences and spread for a hypothetical native and nonnative species with similar numbers of observed occurrences. (*a*) A native species has already had time to disperse into and fill in its range, resulting in opportunities to spread predominantly at range margins. With climate change, spread directions (*blue arrows*) are typically poleward. (*b*) Nonnative species are often introduced into multiple suitable locations by humans (human-mediated introduction; *solid black arrows*). Secondary spread is due to human-mediated long-distance dispersal within the introduction region (*dashed arrows*) or natural dispersal (*red arrows*), which could happen in any direction (and is not only climate driven). These advantages enable faster spread rates for nonnative species.

support common nonnative traits of rapid growth and prolific reproduction (Jauni et al. 2015), which would result in rapid spread. Consequently, spread rates of nonnative populations are likely a combination of both natural dispersal and human-mediated secondary spread, with humans disproportionately responsible for secondary introductions that occur through long-distance dispersal events (**Figure 2*b***) (Suarez et al. 2001). For example, nonnative plants are commonly transported across long distances as ornamentals and often introduced into cooler climates at higher latitudes, giving them an advantage with a warming climate (Bradley et al. 2012, Van der Veken et al. 2008).

Overall, human-mediated introduction enables the rapid movement of species across thousands of kilometers. For the groups included in our analyses, human-mediated introduction led to spread rates several orders of magnitude higher than native species' spread rates. Furthermore, the secondary spread of nonnative species (which might still have included some level of human mediation) was much faster than the spread of native species (**Figure 1**) (Seebens et al. 2021). Human introductions provide an enormous advantage to the ability of nonnative species to keep up with climate change.

Potential range: the geographic range suitable for a species determined by relating occurrences in the species range to environmental conditions to estimate where a species could occur, under either current or future climate change scenarios

Species distribution model (SDM): a geographic representation of a species' niche created by combining species occurrence data with environmental information

4. PROJECTED CHANGES IN SPECIES DISTRIBUTIONS

In addition to observations of how quickly species are able to spread, another key component of whether climate change creates an advantage for nonnative species is how much habitat is available for them to spread into. Predictions of potential range often rely on species distribution models (SDMs; also known as ecological niche models), which aim to create a geographic representation of a species' niche by combining species occurrence data with environmental information (Elith & Leathwick 2009). Because climate is a key driving factor of distributions (Pearson & Dawson

2003, Whittaker 1970), particularly across broad regions, many of these models rely on climate predictors. SDMs have often been used to predict range shifts under future climate conditions (e.g., Allen & Bradley 2016, Gallardo et al. 2017, Warren et al. 2018), providing projections of the potential distributions of both native and nonnative species with climate change.

To assess whether native and nonnative species differ in their potential ranges, we searched the literature for SDM studies projecting current and future ranges for native and nonnative taxa. Unexpectedly, few studies included both groups, instead focusing on one or the other (e.g., Allen & Bradley 2016, Gallardo et al. 2017, Warren et al. 2018). In order to avoid biased comparisons associated with different modeling approaches, data sources, climate scenarios, and timelines, we focus on data sets from three studies that used the same distribution modeling approach for both native and nonnative taxa to examine the projected effect of climate change on the ranges of North American seed plants (Zhang et al. 2017), European fish (Radinger & García-Berthou 2020), and North American birds (Langham et al. 2015). For each study, we identified taxa as either native or nonnative to the study region and extracted each species' modeled current range extent, area of habitat gained versus lost, and future range extent. In all three studies, future ranges were predicted for the year 2050 under comparable emissions scenarios resulting in ∼2°C of warming (**Supplemental Appendix 2**). Our final data set included range sizes for 4,406 native and 681 nonnative plants (Zhang et al. 2017), 458 native and 10 nonnative birds (Langham et al. 2015), and 11 native and 5 nonnative fish (Radinger & García-Berthou 2020). All studies assumed that species (both native and nonnative) could shift into all available projected habitats.

From these case studies, birds and fish were projected to experience a net expansion with climate change on average, while plants were predicted to experience a net contraction (**Figure 3**). However, the average magnitude of the respective range expansion or contraction differed by species origin. Nonnative birds were projected to expand more than native birds, as they have a much larger modeled area of habitat gain than of habitat loss. Nonnative plants were projected to contract less than native plants, driven by the larger extent of area gained relative to native plants. Habitat loss and gain was very similar for nonnative and native fish, although nonnative fish were projected to experience smaller gains and smaller losses than native fish. Overall, nonnative species were projected to have more or similar habitat availability with climate change relative to native species, by either gaining more suitable habitat (birds), contracting less (plants), or remaining the same (fish).

Across all three taxonomic groups, future potential range size was strongly correlated with current potential range size (Pearson's correlation coefficient: birds, $r = 0.95$; fish, $r = 0.75$; plants, $r = 0.90$). Accordingly, species with large potential range sizes, regardless of origin, were more likely to have large areas of expansion and contraction with climate change. Although we did not test for differences in potential range sizes between nonnative and native birds and fish because sample sizes were too small, there was a large difference in range size between native and nonnative plants. Nonnative plants had average potential range sizes 120–130% larger than those of native plants (current range ± SD: native plants, 2,973 ± 2,694 km^2; nonnative plants, 3,586 ± 2,727 km^2; future range ± SD: native plants, 2,537 ± 3,131 km^2; nonnative plants, 3,317 ± 3,817 km^2).

5. WHY MIGHT RANGE EXPANSION BE GREATER FOR NONNATIVE SPECIES?

5.1. Potential Range Changes Suggest an Advantage for Nonnative Species

Nonnative species are projected to have larger range expansion and/or smaller range contraction than native species with climate change, leading to a net advantage for nonnative species

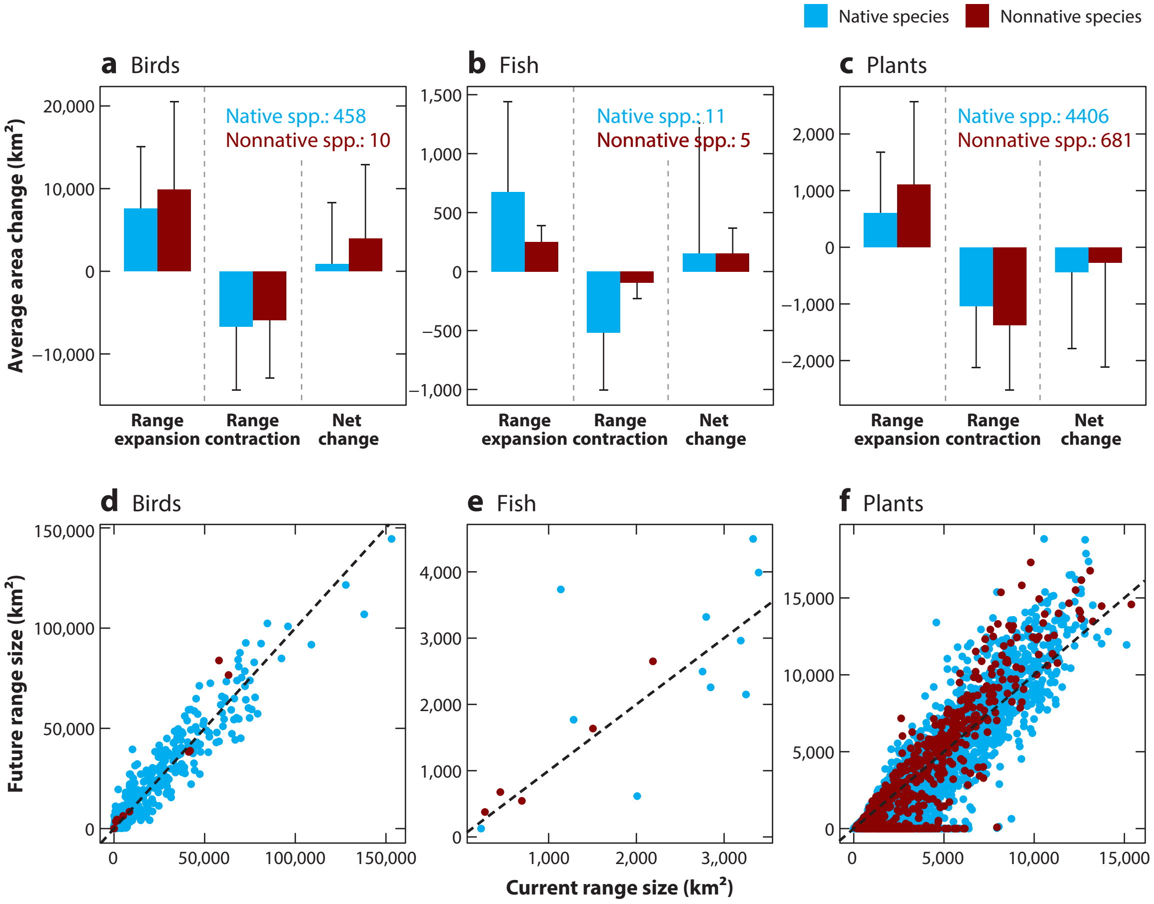

Figure 3

The extent of area gained, area lost, and the net change in range size taken as an average (mean ± SD km^2) across native and nonnative (*a*) birds, (*b*) fish, and (*c*) plants. Sample sizes are shown at the top. (*d–f*) Regardless of origin, species' future potential range size is strongly correlated with current potential range size. The 1:1 line delineates species that are projected to experience a net expansion (above the line) versus contraction (below the line) with climate change.

(**Figure 3**). This pattern appears robust in plants, although given the small sample sizes of the data sets for birds and fish, it is unclear whether our findings for relative range expansion are widespread across other animal taxa. For nonnative plants, greater range expansion relative to range contraction could stem from preadaptation to a warmer climate because nursery plant imports to the United States tend to come from warmer origins (Bradley et al. 2012). For nonnative plants and fish, the inclusion of land use or land cover in addition to climate in the distribution models (Radinger & García-Berthou 2020, Zhang et al. 2017) creates a better representation of nonnative species' potential range because they are often associated with human-modified landscapes (Ibáñez et al. 2009, Vilà & Ibáñez 2011). The combination of changes in climate and human land use may further advantage nonnative species.

Both native and nonnative species are projected to experience some area of range expansion with climate change (**Figure 3**). Depending on the taxon, the expanded range area could be hundreds to thousands of square kilometers, representing large potential for range expansion regardless of origin. However, it is important to consider these projections in the context of species' observed ability to spread, which is an indicator of whether the species can actually get to the new habitat created by climate change. Nonnative species are clearly more likely to be able to disperse into new areas (**Figure 1**), which gives them a huge advantage, given that some form of range expansion is consistently projected across taxa.

Both native and nonnative species are also projected to experience some area of range contraction with climate change (**Figure 3**). Nonnative species contraction has been highlighted as a potential boon for conservation and restoration (Bradley et al. 2009). However, while contraction at warmer range margins has been observed for native species (e.g., Lenoir et al. 2020, Rubenstein et al. 2024), we were unable to find observations of nonnative species range contraction attributable to climate change. The lack of nonnative species contractions may be due to a lack of observations, as the literature tends to focus on nonnative species expansion and associated risk. It is also plausible that nonnative species contractions due to climate change are rare, as high genetic variation in nonnative species populations might enable local adaptation to warmer conditions (Kolbe et al. 2007). The juxtaposition of numerous projections of range contraction with the lack of observations of range contraction for nonnative species highlights an important area for further research.

5.2. Range Size Matters

Although relative range expansion and contraction are certainly important when comparing potential distributions of native and nonnative species, the overall sizes of the species' ranges also affect our interpretation of the magnitude of potential range shifts. Across taxa and origin, and regardless of net gains or losses, we found that the size of a species' future range was strongly associated with the size of its current range (**Figure 3*d–f***). In other words, species with large ranges now will continue to have large ranges with climate change. Range size matters because species with large ranges also tend to have larger potential areas of expansion and contraction (e.g., as seen for nonnative plants in comparison to native plants in **Figure 3*c***). For nonnative species, a large area of expansion can be interpreted as high risk if the nonnative species have the potential to cause negative ecological impacts. Range size could interact with species origin in ways that affect our perception (nonnative species' ranges appear larger than native species' ranges) and the reality (nonnative species' ranges really are larger than native species' ranges) of risk associated with nonnative species.

First, range expansion of nonnative species may appear to be larger because of choices about which types of native and nonnative species are modeled. Studies that model the future ranges of native species tend to focus on rare species because of their high risk of extinction due to their small ranges (e.g., Kremen et al. 2008). In contrast, studies that model the future ranges of nonnative species tend to focus on common species (e.g., Allen & Bradley 2016, Gallardo et al. 2017) because common species have higher potential to cause ecological impact (Catford et al. 2016). Because common species with large ranges also tend to have larger potential range expansion, comparing areas of range expansion for rare native species with small ranges to those of common nonnative species with large ranges makes it seem like nonnative species will expand more. This juxtaposition reinforces the (probably correct) assumption that nonnative species are likely to experience a larger potential range expansion with climate change.

Second, range expansion of nonnative species may be larger because nonnative species have larger ranges (**Figures 2**, **4**). Widespread human-mediated introductions and subsequent secondary spread may allow nonnative species to occupy more climatically suitable areas than native species, leading to a larger potential range. Larger potential ranges may be particularly likely

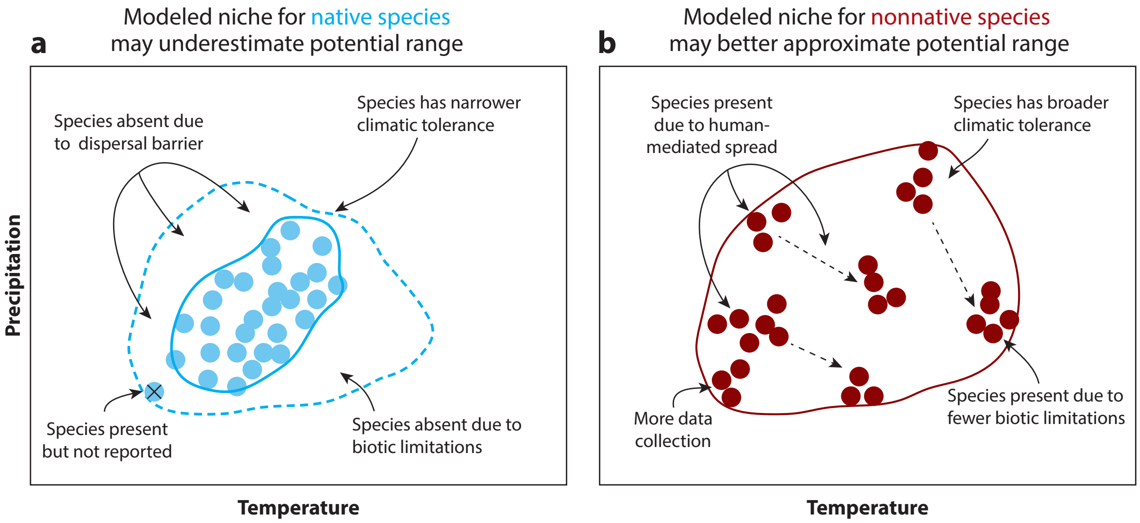

Figure 4

Nonnative species tend to have broader climatic tolerance and inhabit more of their climatic niche than native species with comparable numbers of observations, leading to a larger modeled potential range. (*a*) Native species' occurrences (*blue circles*) fail to encompass parts of their climatic niche (*dashed blue line*) due to dispersal barriers, biotic limitation, and unreported occurrences, leading to a smaller modeled potential range (*solid blue line*). (*b*) Nonnative species often have broader climatic tolerance and species' occurrences (*red circles*) encompass more of their climatic niche due to human-mediated introduction and secondary spread, fewer biotic limitations due to enemy release, and more observations in human-dominated areas, leading to a larger modeled potential range (*solid red line*).

for nonnative species that are intentionally introduced and subsequently released or escape, such as terrestrial animals released for hunting, plants that escape gardens, and herptiles that escape confinement as pets (Hulme et al. 2008). For example, Bradley et al. (2015) showed that SDM predictions for nonnative plants in the continental United States indicated that predicted ranges were 30% larger than those of native plants with comparable numbers of occurrences, likely due to ornamental introductions across broad longitudinal gradients. Similarly, in a meta-analysis, Liu et al. (2020) showed that 80% of 434 animal and plant species exhibited some form of niche expansion in the introduced range, indicating that human-mediated introduction can cause the observed species range to encompass more of its environmental niche.

Larger potential ranges may also be caused by nonnative species tolerating a broader range of climate conditions, on average, than native species (**Figure 4**). For example, in their native ranges, nonnative plants are significantly more widespread and have broader climatic niches than plants that have not established elsewhere (Galán Díaz et al. 2023, Pfadenhauer et al. 2023). Broad climatic tolerance has also been observed in nonnative freshwater (e.g., Bates et al. 2013) and marine species (e.g., Zerebecki & Sorte 2011), which could contribute to a larger potential nonnative range. Similarly, as discussed in the previous section on observed spread, release from natural enemies could enable nonnative species to establish in climate conditions that would otherwise be unavailable due to biotic limitation (**Figure 4**).

Biotic limitation: interactions with other species that limit a species' range by negatively influencing its ability to sustain populations

Lastly, nonnative species ranges may appear larger due to sampling bias in where occurrence data are collected. There may be more records for nonnative species overall because they tend to be prevalent in human modified environments (Vilà & Ibáñez 2011), which are also more likely to be sampled for occurrence records than remote natural areas (Bowler et al. 2022). This potential bias toward occurrence points could result in the locations used to fit models capturing more of the environmental niche of nonnative species than that of native species.

6. CONCLUSIONS

We show that nonnative species have a clear advantage in a changing climate. Human-mediated introduction and secondary spread of nonnative species lead to spread rates that are orders of magnitude faster than those of native species. Compared to the velocity of climate change, nonnative species can readily keep up, while native species are likely to fall behind. Not only are nonnative species spreading more quickly, but they may also have more area available for range expansion with climate change. Our case studies indicate that nonnative species may experience a larger net gain in range size or a smaller net loss, depending on the taxonomic group. Further, given observations of broader environmental tolerance in nonnative species relative to native species, it is likely that nonnative species will have larger potential ranges under current and future climate, leading to more area for range expansion. The combination of rapid spread rates and large potential for range expansion indicates that climate change is likely to preferentially facilitate the persistence and spread of nonnative species over those of native species.

Differences in the observed and potential spread of native and nonnative species have consequences for their management, especially in the face of climate change. While both groups of species have the potential to cause environmental changes as they expand into new areas (Wallingford et al. 2020), the negative ecological impacts of nonnative species are expected to be much larger due to their ecological novelty and traits that increase population growth (Essl et al. 2019). Ironically, as a society we often balk at the risks associated with moving native species just beyond their range margins in response to climate change (McLachlan et al. 2007, Nackley et al. 2017) while blithely moving nonnative species all over the world (Seebens et al. 2017, 2021). Facilitating the movement of nonnative species while failing to assist native species (Breed et al. 2018, Twardek et al. 2023) continues to support the persistence of nonnative species in the face of climate change.

FUTURE ISSUES

1. While observations of spread rates for both native and nonnative species are plentiful, the biological mechanisms that enable species to track climate change (e.g., preadaptation, biological traits, genetic adaptation, enemy release) are often unknown. Greater focus on spread mechanisms would help us to identify vulnerable native and high-risk nonnative species.
2. Surprisingly few studies simultaneously model the potential ranges of both native and nonnative species under current and future climate conditions. More analyses would help to assess comparative range sizes and range shifts across taxonomic groups.
3. Modeling studies use different scenarios, model parameters, and timelines. It is unclear how these differences influence projections of range sizes and range shifts.
4. Model projections of marine species' potential ranges are particularly uncommon.
5. Model projections of nonnative species suggest the potential for range contraction with climate change, but this phenomenon has not been reported observationally.
6. Range shift observations and models suffer from taxonomic and spatial biases. More studies would be beneficial for taxa besides flowering plants and vertebrates and in areas outside of North America and Europe.

7. This review highlights the benefits of assisted migration of native species to enable them to keep up with climate change. However, a dearth of assisted migration experiments leaves unknowns about the sorts of species and recipient ecosystems where this is most appropriate.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

Thanks to J.L. Navarrete, M. Rubenstein, J. Radinger, and S. Sherzai for their help accessing or collecting data. This work was supported by the US Geological Survey Northeast Climate Adaptation Science Center (NE CASC) (award numbers G19AC00091 and G21AC10233-01). Funding was also provided through the Belmont Forum and BiodivERsA joint call for research proposals, under the BiodivScen ERA-NET Cofund program, with funding from the National Science Foundation (ICER-1852060) and the Spanish Ministry of Science, Innovation and Universities (PCI2018-092986 and PCI2018-092939, MCIU/AEI/FEDER, UE). M.V. also acknowledges support from the Europa Excelencia project PREABROAD (EUR2022-134026). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

LITERATURE CITED

Allen JM, Bradley BA. 2016. Out of the weeds? Reduced plant invasion risk with climate change in the continental United States. *Biol. Conserv.* 203:306–12

Bates AE, McKelvie CM, Sorte CJB, Morley SA, Jones NAR, et al. 2013. Geographical range, heat tolerance and invasion success in aquatic species. *Proc. R. Soc. B* 280(1772):20131958

Bayón Á, Vilà M. 2019. Horizon scanning to identify invasion risk of ornamental plants marketed in Spain. *NeoBiota* 52:47–86

Beaury EM, Patrick M, Bradley BA. 2021. Invaders for sale: the ongoing spread of invasive species by the plant trade industry. *Front. Ecol. Environ.* 19(10):550–56

Bellard C, Cassey P, Blackburn TM. 2016. Alien species as a driver of recent extinctions. *Biol. Lett.* 12(2):20150623

Bowler DE, Callaghan CT, Bhandari N, Henle K, Barth MB, et al. 2022. Temporal trends in the spatial bias of species occurrence records. *Ecography* 2022(8):e06219

Bradley BA, Blumenthal DM, Early R, Grosholz ED, Lawler JJ, et al. 2012. Global change, global trade, and the next wave of plant invasions. *Front. Ecol. Environ.* 10(1):20–28

Bradley BA, Early R, Sorte CJB. 2015. Space to invade? Comparative range infilling and potential range of invasive and native plants. *Global Ecol. Biogeogr.* 24(3):348–59

Bradley BA, Laginhas BB, Whitlock R, Allen JM, Bates AE, et al. 2019. Disentangling the abundance–impact relationship for invasive species. *PNAS* 116(20):9919–24

Bradley BA, Oppenheimer M, Wilcove DS. 2009. Climate change and plant invasions: restoration opportunities ahead? *Global Change Biol.* 15(6):1511–21

Breed MF, Harrison PA, Bischoff A, Durruty P, Gellie NJC, et al. 2018. Priority actions to improve provenance decision-making. *BioScience* 68(7):510–16

Burrows MT, Schoeman DS, Buckley LB, Moore P, Poloczanska ES, et al. 2011. The pace of shifting climate in marine and terrestrial ecosystems. *Science* 334(6056):652–55

Capellini I, Baker J, Allen WL, Street SE, Venditti C. 2015. The role of life history traits in mammalian invasion success. *Ecol. Lett.* 18(10):1099–107

Castagné P, Paz-Vinas I, Boulêtreau S, Ferriol J, Loot G, et al. 2023. Patterns of genetic variation in native and non-native populations of European catfish *Silurus glanis* across Europe. *Biodivers Conserv*. 32(6):2127–47

Catford JA, Baumgartner JB, Vesk PA, White M, Buckley YM, McCarthy MA. 2016. Disentangling the four demographic dimensions of species invasiveness. *J. Ecol.* 104(6):1745–58

Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333(6045):1024–26

Clark JS, Lewis M, Horvath L. 2001. Invasion by extremes: population spread with variation in dispersal and reproduction. *Am. Nat.* 157(5):537–54

Clark JS, Silman M, Kern R, Macklin E, HilleRisLambers J. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* 80(5):1475–94

Colautti RI, Grigorovich IA, MacIsaac HJ. 2006. Propagule pressure: a null model for biological invasions. *Biol. Invasions* 8(5):1023–37

Davis MB, Shaw RG. 2001. Range shifts and adaptive responses to quaternary climate change. *Science* 292(5517):673–79

DeWalt SJ, Denslow JS, Ickes K. 2004. Natural-enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. *Ecology* 85(2):471–83

Dobrowski SZ, Parks SA. 2016. Climate change velocity underestimates climate change exposure in mountainous regions. *Nat. Commun.* 7(1):12349

Dukes JS, Mooney HA. 1999. Does global change increase the success of biological invaders? *Trends Ecol. Evol.* 14(4):135–39

Elith J, Leathwick JR. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst.* 40:677–97

Essl F, Dullinger S, Genovesi P, Hulme PE, Jeschke JM, et al. 2019. A conceptual framework for range-expanding species that track human-induced environmental change. *BioScience* 69(11):908–19

Galán Díaz J, De la Riva E, Martín-Forés I, Vilà M. 2023. Which features at home make a plant prone to become invasive? Advancing research on alien species and biological invasions. *NeoBiota* 86:1–20

Gallardo B, Aldridge DC, González-Moreno P, Pergl J, Pizarro M, et al. 2017. Protected areas offer refuge from invasive species spreading under climate change. *Global Change Biol*. 23(12):5331–43

Gallardo B, Clavero M, Sánchez MI, Vilà M. 2016. Global ecological impacts of invasive species in aquatic ecosystems. *Global Change Biol*. 22(1):151–63

González-Moreno P, Diez JM, Richardson DM, Vilà M. 2015. Beyond climate: disturbance niche shifts in invasive species. *Global Ecol. Biogeogr.* 24(3):360–70

Gu S, Qi T, Rohr JR, Liu X. 2023. Meta-analysis reveals less sensitivity of non-native animals than natives to extreme weather worldwide. *Nat. Ecol. Evol.* 7:2004–27

Hänfling B. 2007. Understanding the establishment success of non-indigenous fishes: lessons from population genetics. *J. Fish Biol.* 71(sd):115–35

Hellmann JJ, Byers JE, Bierwagen BG, Dukes JS. 2008. Five potential consequences of climate change for invasive species. *Conserv. Biol.* 22(3):534–43

Horvitz N, Wang R, Wan F-H, Nathan R. 2017. Pervasive human-mediated large-scale invasion: analysis of spread patterns and their underlying mechanisms in 17 of China's worst invasive plants. *J. Ecol.* 105(1):85–94

Hulme PE, Bacher S, Kenis M, Klotz S, Kühn I, et al. 2008. Grasping at the routes of biological invasions: a framework for integrating pathways into policy. *J. Appl. Ecol.* 45(2):403–14

Hutchinson GE. 1957. Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.* 22:415–27

Ibáñez I, Silander JA Jr., Allen JM, Treanor SA, Wilson A. 2009. Identifying hotspots for plant invasions and forecasting focal points of further spread. *J. Appl. Ecol.* 46(6):1219–28

IPCC (Intergov. Panel Clim. Change). 2023. *Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. IPCC, Geneva, Switz.

Jackson ST, Overpeck JT, Webb T III, Keattch SE, Anderson KH. 1997. Mapped plant-macrofossil and pollen records of late quaternary vegetation change in Eastern North America. *Quat. Sci. Rev.* 16(1):1–70

Jacobi WR, Hardin JG, Goodrich BA, Cleaver CM. 2012. Retail firewood can transport live tree pests. *J. Econ. Entomol.* 105(5):1645–58

Jauni M, Gripenberg S, Ramula S. 2015. Non-native plant species benefit from disturbance: a meta-analysis. *Oikos* 124(2):122–29

Jeschke JM, Pyšek P. 2018. Tens rule. In *Invasion Biology: Hypotheses and Evidence*, ed. JM Jeschke, T Heger, pp. 124–32. Wallingford, UK: CABI

Kawecki TJ. 2008. Adaptation to marginal habitats. *Annu. Rev. Ecol. Evol. Syst.* 39:321–42

Kolbe JJ, Glor RE, Schettino LR, Lara AC, Larson A, Losos JB. 2007. Multiple sources, admixture, and genetic variation in introduced *Anolis* lizard populations. *Conserv. Biol.* 21(6):1612–25

Kremen C, Cameron A, Moilanen A, Phillips SJ, Thomas CD, et al. 2008. Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. *Science* 320(5873):222–26

Langham GM, Schuetz JG, Distler T, Soykan CU, Wilsey C. 2015. Conservation status of North American birds in the face of future climate change. *PLOS ONE* 10(9):e0135350

Lenoir J, Bertrand R, Comte L, Bourgeaud L, Hattab T, et al. 2020. Species better track climate warming in the oceans than on land. *Nat. Ecol. Evol.* 4(8):1044–59

Lenoir J, Svenning J-C. 2015. Climate-related range shifts—a global multidimensional synthesis and new research directions. *Ecography* 38(1):15–28

Liebhold AM, Brockerhoff EG, Kalisz S, Nuñez MA, Wardle DA, Wingfield MJ. 2017. Biological invasions in forest ecosystems. *Biol. Invasions* 19(11):3437–58

Liu C, Wolter C, Xian W, Jeschke JM. 2020. Most invasive species largely conserve their climatic niche. *PNAS* 117(38):23643–51

Liu H, Stiling P. 2006. Testing the enemy release hypothesis: a review and meta-analysis. *Biol. Invasions.* 8(7):1535–45

Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD. 2009. The velocity of climate change. *Nature* 462(7276):1052–55

Lockwood JL, Welbourne DJ, Romagosa CM, Cassey P, Mandrak NE, et al. 2019. When pets become pests: the role of the exotic pet trade in producing invasive vertebrate animals. *Front. Ecol. Environ.* 17(6):323–30

Maron JL, Vilà M. 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos* 95(3):361–73

Mason RAB, Cooke J, Moles AT, Leishman MR. 2008. Reproductive output of invasive versus native plants. *Global Ecol. Biogeogr.* 17(5):633–40

Mason SC, Palmer G, Fox R, Gillings S, Hill JK, et al. 2015. Geographical range margins of many taxonomic groups continue to shift polewards. *Biol. J. Linnean Soc.* 115(3):586–97

McLachlan JS, Hellmann JJ, Schwartz MW. 2007. A framework for debate of assisted migration in an era of climate change. *Conserv. Biol.* 21(2):297–302

Nackley LL, West AG, Skowno AL, Bond WJ. 2017. The nebulous ecology of native invasions. *Trends Ecol. Evol.* 32(11):814–24

Padilla DK, Williams SL. 2004. Beyond ballast water: aquarium and ornamental trades as sources of invasive species in aquatic ecosystems. *Front. Ecol. Environ.* 2(3):131–38

Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421(6918):37–42

Pearson RG, Dawson TP. 2003. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecol. Biogeogr.* 12(5):361–71

Pecl GT, Araújo MB, Bell JD, Blanchard J, Bonebrake TC, et al. 2017. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* 355(6332):eaai9214

Petsch DK, dos Santos Bertoncin AP, Ortega JCG, Thomaz SM. 2022. Non-native species drive biotic homogenization, but it depends on the realm, beta diversity facet and study design: a meta-analytic systematic review. *Oikos* 2022(6):e08768

Pfadenhauer WG, Bradley BA. 2024. Quantifying vulnerability to plant invasion across global ecosystems. bioRxiv 2024.02.21.581382. **https://doi.org/10.1101/2024.02.21.581382**

Pfadenhauer WG, Nelson MF, Laginhas BB, Bradley BA. 2023. Remember your roots: Biogeographic properties of plants' native habitats can inform invasive plant risk assessments. *Divers. Distrib.* 29(1):4–18

Quintero I, Wiens JJ. 2013. Rates of projected climate change dramatically exceed past rates of climatic niche evolution among vertebrate species. *Ecol. Lett.* 16(8):1095–103

Radinger J, García-Berthou E. 2020. The role of connectivity in the interplay between climate change and the spread of alien fish in a large Mediterranean river. *Global Change Biol.* 26(11):6383–98

Rapoport EH. 2000. Remarks on the biogeography of land invasions. *Rev. Chil. Hist. Nat.* 73(2):367–80

Reichard SH, White P. 2001. Horticulture as a pathway of invasive plant introductions in the United States: Most invasive plants have been introduced for horticultural use by nurseries, botanical gardens, and individuals. *BioScience* 51(2):103–13

Resasco J, Haddad NM, Orrock JL, Shoemaker D, Brudvig LA, et al. 2014. Landscape corridors can increase invasion by an exotic species and reduce diversity of native species. *Ecology* 95(8):2033–39

Rilov G, Galil B. 2009. Marine bioinvasions in the Mediterranean Sea – history, distribution and ecology. In *Biological Invasions in Marine Ecosystems: Ecological, Management, and Geographic Perspectives*, ed. G Rilov, JA Crooks, pp. 549–75. Berlin, Heidelberg: Springer

Rius M, Darling JA. 2014. How important is intraspecific genetic admixture to the success of colonising populations? *Trends Ecol. Evol.* 29(4):233–42

Roy HE, Pauchard A, Stoett P, Renard Truong T, Bacher S, et al. 2023. *IPBES Invasive Alien Species Assessment: Summary for Policymakers*. IPBES Secr., Bonn, Germany. **https://doi.org/10.5281/zenodo.10127924**

Rubenstein MA, Weiskopf SR, Bertrand R, Carter SL, Comte L, et al. 2024. *CoRE (Contractions or Range Expansions) Database: Global Database of Species Range Shifts from 1802–2019*. US Geological Survey, Reston, VA, updated Mar. 29. **https://doi.org/10.5066/P99VP2TW**

Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, et al. 2017. No saturation in the accumulation of alien species worldwide. *Nat. Commun.* 8(1):14435

Seebens H, Blackburn TM, Hulme PE, van Kleunen M, Liebhold AM, et al. 2021. Around the world in 500 years: inter-regional spread of alien species over recent centuries. *Global Ecol. Biogeogr.* 30(8):1621–32

Simberloff D. 2000. Global climate change and introduced species in United States forests. *Sci. Total Environ.* 262(3):253–61

Smith AL, Hodkinson TR, Villellas J, Catford JA, Csergő AM, et al. 2020. Global gene flow releases invasive plants from environmental constraints on genetic diversity. *PNAS* 117(8):4218–27

Somero GN. 2010. The physiology of climate change: How potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers.' *J. Exp. Biol.* 213(6):912–20

Sorte CJB, Williams SL, Carlton JT. 2010. Marine range shifts and species introductions: comparative spread rates and community impacts. *Global Ecol. Biogeogr.* 19(3):303–16

Suarez AV, Holway DA, Case TJ. 2001. Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. *PNAS* 98(3):1095–100

Tallamy DW, Shropshire KJ. 2009. Ranking lepidopteran use of native versus introduced plants. *Conserv. Biol.* 23(4):941–47

Theoharides KA, Dukes JS. 2007. Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytologist* 176(2):256–73

Torchin ME, Mitchell CE. 2004. Parasites, pathogens, and invasions by plants and animals. *Front. Ecol. Environ.* 2(4):183–90

Twardek WM, Taylor JJ, Rytwinski T, Aitken SN, MacDonald AL, et al. 2023. The application of assisted migration as a climate change adaptation tactic: an evidence map and synthesis. *Biol. Conserv.* 280:109932

USFWS (US Fish Wildl. Serv.). 2023. *Endangered and Threatened Wildlife and Plants; Designation of Experimental Populations*. 88 FR 42642, USFWS, Washington, DC. **https://www.federalregister.gov/documents/2023/07/03/2023-13672/endangered-and-threatened-wildlife-and-plants-designation-of-experimental-populations**

Václavík T, Meentemeyer RK. 2012. Equilibrium or not? Modelling potential distribution of invasive species in different stages of invasion. *Divers. Distrib.* 18(1):73–83

Van der Veken S, Hermy M, Vellend M, Knapen A, Verheyen K. 2008. Garden plants get a head start on climate change. *Front. Ecol. Environ.* 6(4):212–16

van Kleunen M, Bossdorf O, Dawson W. 2018a. The ecology and evolution of alien plants. *Annu. Rev. Ecol. Evol. Syst.* 49:25–47 van Kleunen M, Essl F, Pergl J, Brundu G, Carboni M, et al. 2018b. The changing role of ornamental horticulture in alien plant invasions. *Biol. Rev.* 93(3):1421–37

Vilà M, Dunn AM, Essl F, Gómez-Díaz E, Hulme PE, et al. 2021. Viewing emerging human infectious epidemics through the lens of invasion biology. *BioScience* 71(7):722–40

Vilà M, Ibáñez I. 2011. Plant invasions in the landscape. *Landscape Ecol.* 26(4):461–72

Vu Ho K, Kröel-Dulay G, Tölgyesi C, Bátori Z, Tanács E, et al. 2023. Non-native tree plantations are weak substitutes for near-natural forests regarding plant diversity and ecological value. *Forest Ecol. Manag.* 531:120789

Wallingford PD, Morelli TL, Allen JM, Beaury EM, Blumenthal DM, et al. 2020. Adjusting the lens of invasion biology to focus on the impacts of climate-driven range shifts. *Nat. Clim. Chang.* 10(5):398–405

Warren R, Price J, Graham E, Forstenhaeusler N, VanDerWal J. 2018. The projected effect on insects, vertebrates, and plants of limiting global warming to 1.5°C rather than 2°C. *Science* 360(6390):791–95

Whittaker RH. 1970. *Communities and Ecosystems*. London: Macmillan

Williams JW, Jackson ST, Kutzbach JE. 2007. Projected distributions of novel and disappearing climates by 2100 AD. *PNAS* 104(14):5738–42

Willis CG, Ruhfel BR, Primack RB, Miller-Rushing AJ, Losos JB, Davis CC. 2010. Favorable climate change response explains non-native species' success in Thoreau's woods. *PLOS ONE* 5(1):e8878

Willis KJ, MacDonald GM. 2011. Long-term ecological records and their relevance to climate change predictions for a warmer world. *Annu. Rev. Ecol. Evol. Syst.* 42:267–87

Zerebecki RA, Sorte CJB. 2011. Temperature tolerance and stress proteins as mechanisms of invasive species success. *PLOS ONE* 6(4):e14806

Zhang J, Nielsen SE, Chen Y, Georges D, Qin Y, et al. 2017. Extinction risk of North American seed plants elevated by climate and land-use change. *J. Appl. Ecol.* 54(1):303–12

Zhao Y-Z, Liu M-C, Feng Y-L, Wang D, Feng W-W, et al. 2020. Release from below- and aboveground natural enemies contributes to invasion success of a temperate invader. *Plant Soil* 452(1):19–28