Research paper

Climate space, traits, and the spread of nonnative plants in North America

Qinfeng Guo [a, *], Hong Qian [b], Shenhua Qian [c, d]

[a] USDA FS — Southern Research Station, 3041 E. Cornwallis Road, Research Triangle Park, NC 27709, USA
[b] Research and Collections Center, Illinois State Museum, 1011 East Ash Street, Springfield, IL 62703, USA
[c] Key Laboratory of the Three Gorges Reservoir Region's Eco-Environment, Ministry of Education, Chongqing University, Chongqing 400045, China
[d] College of Environment and Ecology, Chongqing University, Chongqing 400045, China

ARTICLE INFO

ABSTRACT

The future distribution of invading species depends on the climate space available and certain life history traits that facilitate invasion. Here, to predict the spread potential of plant species introduced in North America north of Mexico (NAM), we compiled distribution and life history data (i.e., seed size, life form, and photosynthetic pathways) for 3021 exotic plant species introduced to NAM. We comparatively examined the species' range size and climate space in both native and exotic regions and the role of key life history traits. We found that large climate space for most exotic plants is still available in NAM. The range sizes in global exotic regions could better predict the current range sizes in NAM than those in global native regions or global native plus exotic regions. C3 species had larger ranges on average than C4 and CAM plants, and herbaceous species consistently showed stronger relationships in range size between native and exotic regions than woody species, as was the case within the C3 species group. Seed size was negatively related to range size both in native regions and in NAM. However, seed size surprisingly showed a positive correlation with global exotic range size and no correlation with the current actual global (native plus exotic) range size. Our findings underline the importance of species' native distribution and life history traits in predicting the spread of exotic species. Future studies should continue to identify potential climate space and use underappreciated species traits to better predict species invasions under changing climate.

1. Introduction

The introduction and spread of nonnative (introduced, alien, exotic) species continue to cause enormous ecological and economic damage. It has long been commonly perceived that climates predominantly limit the distributions of most species worldwide (Thomas, 2010). However, accumulating new evidence in the past 2—3 decades shows that the current geographical distributions of many species in their native regions are not a result of the limitations of the climate. Nevertheless, although many, if not most, species could only occupy their partial (inner) climate space, climate space would still set the outer limits for species distribution (Petitpierre et al., 2012). Therefore, identifying the climate space available for a species is urgently needed to project its potential distribution in the future, not only for native species (for conservation purposes) but also for introduced/invading species (for management purposes) (Gallien et al., 2010; Sychrová et al., 2022).

In practice, however, identifying a species' climate space (envelope) and predicting future invasions is not an easy task (Bradley et al., 2010), mainly because a species' range could also be limited or affected by many non-climate factors (Richardson et al., 1994), which include biotic factors such as life history, dispersal, and genetic flexibility (Ricklefs et al., 2008; Whitney and Gabler, 2008; Nunez-Mir et al., 2019), and abiotic factors such as geographical barriers. Yet, for introduced species, distribution and associated climate conditions from native regions are very informative and can be used in projecting exotic distributions (Reichard and Hamilton, 1997; Guo et al., 2006; Ricklefs et al., 2008; Albright et al., 2010; van Kleunen et al., 2015; Hock et al., 2020).

Using the native distribution of a species as a powerful tool to predict the spread and distribution of the species in exotic regions is a common practice (Guo, 2006; Broennimann et al., 2007; Williamson et al., 2009; Rejmánek, 2014; Casado et al., 2018; Hock et al., 2020; Sychrová et al., 2022; Liu et al., 2023). This approach has long been used in intentional species introductions (Pearson et al., 2022) and human-assisted species migration (McLachlan et al., 2007) because it has been commonly perceived that species from the similar climates may be easier to survive and naturalize after introduction. However, such an approach has been increasingly challenged by accumulating evidence that native and exotic distributions of the same species often do not match, especially in the climate space they occupy (Broennimann et al., 2007). Such mismatches are primarily due to the effects of non-climate factors such as the initial location of introduction, time since introduction, and altered interactions with different sets of coexisting species. Residence time is especially important because it is closely linked to the spread and distribution of introduced species, many still spreading in their exotic regions (Williamson et al., 2009).

To date, the most frequently used climate variables in predicting the spread of invasive species include mean annual temperature (MAT) (Dangles et al., 2008) and mean annual precipitation (MAP), which are the two most important predictors of species distribution, especially for plants (Petitpierre et al., 2012), and are the sole climatic variables used to define biomes (Whittaker, 1975). The studies examining latitudinal shifts in species invasions (Guo et al., 2012; Zhang et al., 2023) have associated the findings with climatic niche shifts (Early and Sax, 2014; Atwater et al., 2018). A key question in predicting further invasions, however, remains largely under-explored: How much climate space in MAT and MAP is still available for invaded species in an exotic region such as North America to match those in global native regions? To answer such questions, integrated information regarding current distribution (location and range size) and related underlying climate data in both native and exotic regions is needed.

Because of the close links between certain plant traits, such as seed size and species distribution (range size) in native regions (e.g., Guo et al., 2000; Jandt et al., 2021) and because the invasiveness of introduced species shows phylogenetic relatedness among species (Qian et al., 2022; Qian, 2023a, 2023b, 2023c; Qian and Deng, 2024), many studies have attempted to use similar traits (e.g., Reichard and Hamilton, 1997; Goodwin et al., 1999; Nunez-Mir et al., 2019; Gioria et al., 2023) and phylogenetics (Pyšek, 1998) to predict species invasiveness and spread in exotic regions (Ricklefs et al., 2008; Garcia et al., 2014). Not only does one can use native distributions to predict exotic distributions, but one can also use distributions in other exotic regions to predict the actual and potential distributions in a particularly concerned region such as North America. There are different ways to classify plant species based on certain traits and functions, but each could offer different and sometimes unique insights into the mechanisms of plants' responses to environmental change. In terms of responses to climate change, classifications using photosynthetic pathways and life/growth forms might be especially meaningful. For example, previous studies have shown that C3, C4, and CAM plants show different sensitivities to climate change (e.g., warming and increases in atmosphere CO_2 concentration) (Ehleringer and Monson, 1993; Hamilton III et al., 2008; Jia et al., 2016). Early studies also show that woody species have accumulated fewer changes per million years in climatic niche space than related herbaceous species (Smith and Beaulieu, 2009). Also, the climate space used by woody species is usually smaller than sister herbaceous species (Smith and Beaulieu, 2009). It would be useful to test in the future whether and to what extent relevant information from native species may be applied to exotic species.

Although new studies continue to show that the current distributions of many species are not limited by climate factors alone, it is still largely unknown what proportion and which of the nonnative species in an exotic region are indeed not constrained by climates. Also, the role of life history traits in species invasions and possible effects of climate change continue to generate inconsistencies and inconclusive results. We address the following questions using data from 3021 globally introduced plant species in North America north of Mexico (hereafter NAM which includes the continental United States and Canada) from the rest of the world (Figs. S1 and S2). (1) To what degree native and exotic distributions around the globe can predict invaded (exotic) distribution in NAM? (2) How much potential climate space is still available for exotic plant species naturalized in NAM? (3) Can certain life history traits such as photosynthetic pathways, seed size, and life forms explain species distribution (range size) better in native than in exotic regions (Rejmánek and Richardson, 1996)? Answers to these questions are urgently needed for basic ecology and invasive species management.

2. Methods

Naturalization is one of the stages of the introduction–naturalization–invasion continuum (Blackburn et al., 2011; Richardson and Pyšek, 2012). North America has been invaded by more naturalized exotic plant species than any other continent (Pyšek et al., 2017). We compiled distribution data for 3021 exotic plant species introduced from the rest of the world to continental North America north of Mexico (hereafter NAM). These species were considered naturalized in NAM (van Kleunen et al., 2019). Native and nonnative distributions of these species were obtained from van Kleunen et al. (2019) and the World Checklist of Vascular Plants (Brown et al., 2023). The operational geographical units used to document species distributions are geographical units at level 3 of the scheme of the International Working Group on Taxonomic Databases for Plant Sciences (Brummitt, 2001). Oceanic islands and Antarctica were excluded. We used the package U.Taxonstand (Zhang and Qian, 2023) to standardize botanical nomenclature according to the World Checklist of Vascular Plants. Native and nonnative range sizes of each species were estimated according to the operational geographical units where the species was present (i.e., the total area of the operational geographical units in which the species occurred in either case).

We acquired climate data (bio1 and bio12 for MAT and MAP, respectively) from the CHELSA climate database (https://chelsa-climate.org) (Karger et al., 2017). We calculated the average value of either climatic variable based on all pixels at the 30-arc-second resolution located within the distributional range of a species within each geographical region defined in van Kleunen et al. (2019).

To evaluate the climate spaces of the introduced species, we divided the global terrestrial regions into 300 km × 300 km grid cells based on the Mollweide (equal-area) projection. We chose this broad spatial resolution to document climatic data to better match the spatial scale of the geographical units used to document plant distributions used in this study. We calculated the average value of MAT or MAP based on all pixels at the 30-arc-second resolution within each grid cell. After excluding the grid cells with < 50% of land or no plant species, a total of 1469 grid cells were included in this study, 261 of which were located in NAM.

To investigate whether the ratio of the nonnative range of a species to the overall (i.e., native plus nonnative) range of the species is constrained by phylogenetic relationships of species, we used Pagel's λ (Pagel, 1999) to assess whether there is a significant phylogenetic signal in the ratio of the nonnative range of a species

to the overall range of the species, using the function phylosig in the package phytools (Kembel et al., 2010). A value of 0 indicates no phylogenetic signal in the ratio across the phylogeny, whereas a value of 1 indicates a strong phylogenetic signal, which matches expectations under the Brownian motion model. The significance of Pagel's λ was assessed based on 1000 randomizations. We used the megatree "GBOTB.extended.WCVP.tre" as a backbone and the functions build.nodes.1 and Scenario 3 in the package U.Phylo-Maker (Jin and Qian, 2023) to add species to the megatree, and pruned the resulting phylogeny to retain only the 3021 species examined in this study.

We used linear regression analyses to examine the relationships between native and exotic range sizes. These relationships were separately explored between global native regions and exotic region NAM, between global native and global exotic regions, and between global exotic (excluding NAM) and exotic region NAM. Mann−Whitney Rank Sum Tests were adopted to examine the post-naturalization changes in mean range size (i.e., the relative range size in native and exotic regions). This was done for paired comparisons between the two life forms (woody vs. herbaceous species) and among the three photosynthetic pathways, i.e., between C3 and C4, between C3 and CAM, and between C4 and CAM.

To examine how life history traits may influence the native−exotic range size relationships, we collated the life history data for seed size, life form (woody vs. herbaceous), and three photosynthetic pathways (C3, C4, and CAM) from multiple sources, including online traits databases (https://plants.usda.gov/home) and regional floras such as the Flora of North America, Flora of China, and Centre for Agriculture and Bioscience International (CABI), with more complete life history data for 2441 species (Figs. S1 and S2).

The effects of seed size were examined for global native, global exotic, global native plus exotic, and NAM, respectively. To examine the detailed responses in range size and possible mechanisms related to climate, we grouped all the exotic plant species based on life form (i.e., herbaceous vs. woody species) and photosynthetic pathways (i.e., C3, C4, and CAM) because they may show different sensitivities to climate fluctuation. To confirm the findings related to the spatial spread of different life forms in exotic regions for all 2031 plant species, we also divided all C3 species into woody and herbaceous species and made comparisons between the two life forms. We did not do this for C4 and CAM plants as there were very few woody species for comparison in these two plant groups.

3. Results

3.1. Native vs. exotic distributions

The ratio of nonnative range size to the overall (native plus nonnative) range size of a species varied greatly from 0.016 to 0.995, with the mean and SD of the ratio for the 3021 species being 0.513 ± 0.276. We found a significant phylogenetic signal in the ratio of nonnative range size to overall range size (Pagel's $\lambda = 0.644$, $P < 0.0001$), suggesting that closely related species have similar ratios of nonnative range sizes to overall range sizes (Fig. 1).

Among the 3021 exotic plant species, 215 were introduced to continental NAM only (i.e., NAM exotic range areas ≈ global exotic range areas). Most herbaceous exotic plants were introduced to NAM from Europe, and the majority of most woody species were introduced from Asia and Europe (Figs. S1a and b). The majority of C3 and CAM plants were also from Europe, but most C4 plants were from Asia and Africa (Figs. S1c, d, e). As expected, to some extent, most of the herbaceous plants were found at higher latitudes in NAM than woody plants, and both groups were mostly on the east
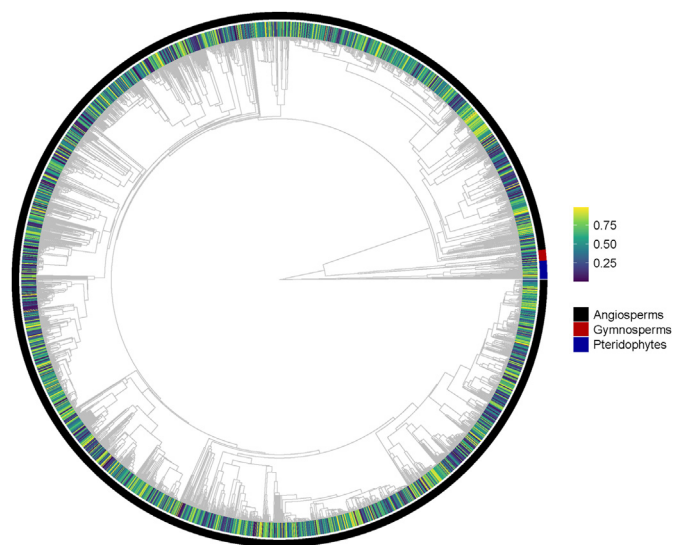

Fig. 1. Variation (indicated by colored lines) in the ratio of the exotic range size to the overall (native plus exotic) range size across the phylogeny of the 3021 exotic plant species introduced from the rest of the world to North America north of Mexico (NAM).

and west coasts. Also, C3 and, to a lesser extent, CAM plants were distributed at higher latitudes than C4 plants (Fig. S2).

At the global scale, 1265 (42%) species already had larger global exotic ranges than their native ranges (Fig. 2a). Although NAM (24,709,000 km^2) only occupies 19% of the entire global terrestrial region (129,777,684 km^2), 378 out of the 3021 (15%) exotic plant species already had larger range sizes in NAM alone than their native ranges (the species above the $y = x$ line in Fig. 2a; see also Fig. S3 and Appendix S1). Species rank and dominance curves based on range size shifted between native and exotic regions; that is, relative to their native regions, many more introduced species had very small ranges (Fig. S4).

NAM exotic range sizes showed a positive relationship with global native range sizes, but the relationship with global (except NAM) exotic range sizes was stronger (Fig. 2a and b). However, the global native and exotic range sizes are positively correlated. The positive correlation is constrained by the diagonal $y = -x$ line; that is, when native ranges are very large, it is impossible for global exotic ranges to be very large also (due to fixed global land area, i.e., when a species' native range is very large, its potential exotic region becomes limited (Fig. 2c).

All plant groups (C3, C4, CAM, herbaceous, woody) showed positive relationships between native and NAM (exotic) range sizes. However, the slopes of the relationships between native and NAM range sizes were not significantly different among these plant groups (in all cases, $P > 0.05$; Fig. 3a and b). Nevertheless, taken together and on average, all plant groups considered here (i.e., C3, C4, CAM; herbaceous vs. woody) still had larger ranges in native than in NAM, mainly because the exotic region in NAM is smaller than the native regions (Fig. 3c and d).

In the native regions, C3 species had much smaller ranges than C4 species (as expected, Mann−Whitney Rank Sum Test, $T = 205573$, $P < 0.001$) but larger ranges than CAM plants ($T = 64828$, $P < 0.001$) which had about 1/3 of range sizes of C4 plants ($T = 8532$, $P < 0.001$). In NAM, however, there was no significant difference in range size between C3 and C4 plants ($T = 158772$, $P = 0.482$), but both groups had significantly larger ranges than CAM plants (C3 vs. CAM, $T = 66061$, $P < 0.001$; C4 vs. CAM, $T = 10835$, $P = 0.007$; Fig. 3c). Therefore, in comparison, C3 species clearly increased their range sizes in NAM more significantly than C4 and CAM species (Figs. 3c and S5).
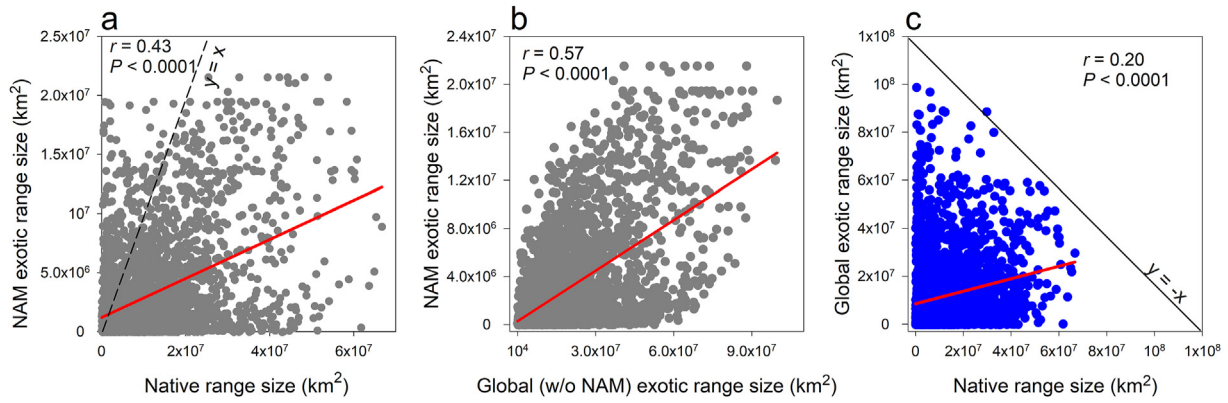
Fig. 2. The relationships among native and exotic range sizes of the 3021 exotic introduced species in North America north of Mexico (NAM). (**a**) Global native vs. exotic NAM; (**b**) Global exotic (excluding NAM) vs. NAM: global exotic ranges could better predict the exotic range size in NAM than global native ranges; (**c**) Global native vs. global exotic: Although the global native and exotic range sizes are positively correlated to each other, the positive correlation is constrained by the diagonal $y = -x$ line; that is, when native ranges are very large, it is impossible for global exotic ranges to be very large also (due to fixed global land area).
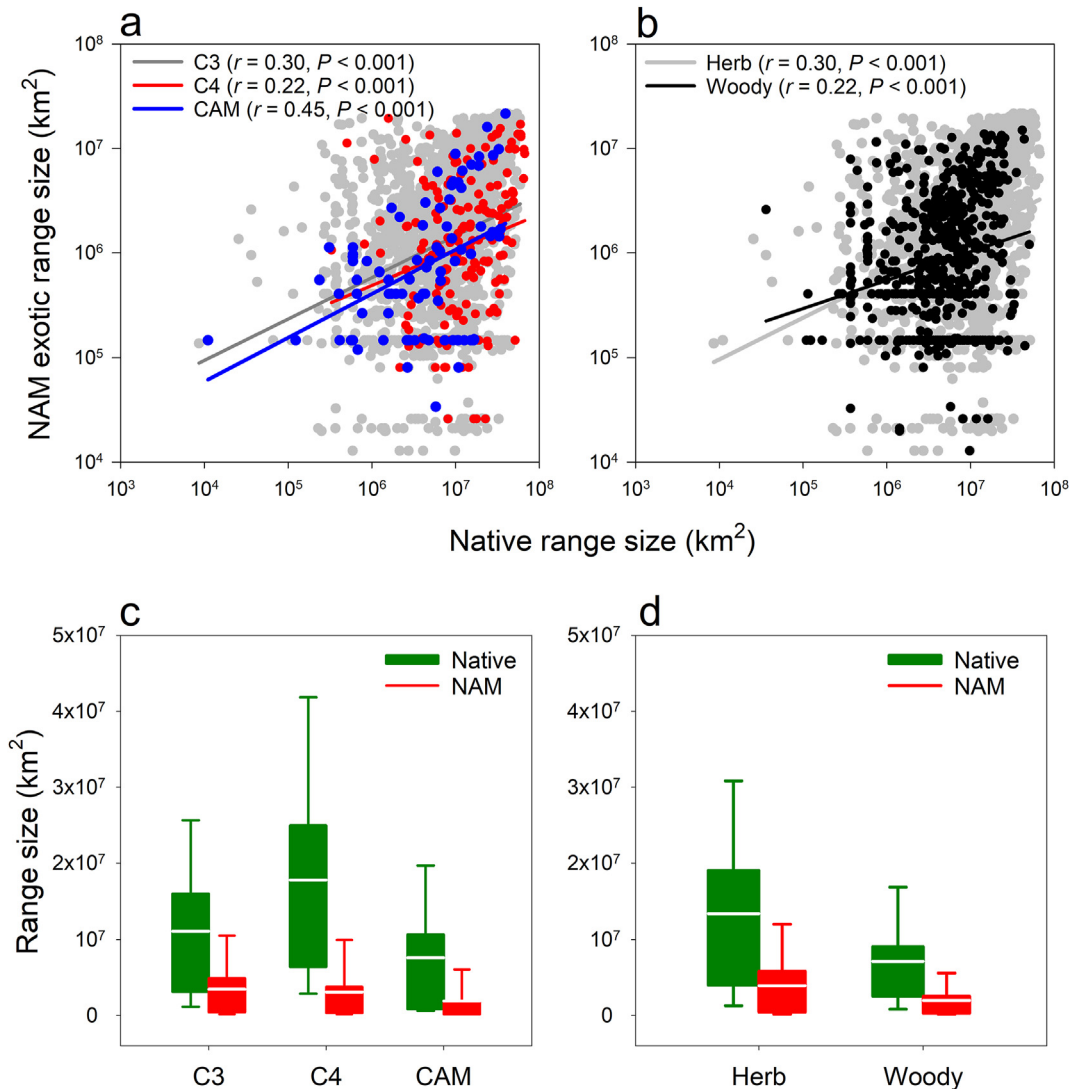

Fig. 3. Comparisons in range size in native vs. exotic regions of the introduced plants in North America north of Mexico (NAM). There are significant positive relationships between native and exotic range size in NAM for various exotic plant groups based on (**a**) photosynthetic pathways (C3, C4, and CAM) and (**b**) life/growth form (herbaceous vs. woody). There are also differences in range size among plant groups (**c**, **d**) and between their native and exotic regions in NAM. The horizontal lines in the boxes are mean values. The boxes in **c** and **d** represent the 25th and 75th percentiles. The solid line in the box is the mean, and the whiskers are error bars (the 95% confidence interval).

In both native and exotic (NAM) regions, herbaceous plants had larger ranges than woody plants (Mann−Whitney Rank Sum Test, $T = 441104$, $P < 0.001$ and $T = 488878$, $P < 0.001$, respectively; Figs. 3d and S5). However, herbaceous species constantly exhibited stronger relationships in range size between native and exotic regions (Fig. 3b). Similarly, among C3 species, herbaceous species also showed stronger relationships in range size between native and exotic regions than woody species (Fig. S6).

3.2. Climate space and life history traits

Among the 3021 species, 444 already occupy ranges in NAM with maximum MATs greater than that in their native regions, 1405 occupied ranges in which minimum MATs were lower than in their native regions, 661 exceeded the maximum MAPs found in the native regions, and 493 had minimum MAPs lower than in their native regions. The corresponding figures were much larger in global exotic regions (including NAM), i.e., 1342 had already exceeded the maximum MAT found in their native regions, 1767 had lower minimum MAT than that in their native regions, 1701 exceeded their native regions' maximum MAP, and 1105 had lower minimum MAP than that in their native regions.

Many of the 3021 species shifted their ranges toward colder places within the potential climate space (i.e., poleward shifts), especially C3 species (Fig. 4). In general, the 3021 species used more temperature space (MAT), but not precipitation space (MAP), especially where precipitation was very low (i.e., mostly the southwestern deserts; Fig. 4). The estimated climate space based on climate conditions across the 261 grids in NAM also indicated more climate space is still available for further spread of most exotic

Fig. 4. Species-based climate space filling across the global (native) and NAM (exotic) by the 3021 introduced plant species in continental North America. The gray and red lines represent the ranges of MAT and MAP centered at the mean values of the 3021 exotic species used in their native and NAM, respectively. Blue symbols represent the estimated climate space across 261 grids (i.e., grid-based) in NAM. The difference between blue squares and red lines thus indicates the potential climate space for further spread in NAM in the future. The min MATs of some exotic plants in NAM seem to be reaching or exceeding their limits, although the southern part of NAM has higher exotic richness. The 3021 exotic species now occupy only a narrow range of potential precipitation gradients (MAP).

species (as indicated by the difference between blue and red symbols in Fig. 4).

On average, the ranges currently occupied by exotic plants in NAM still use smaller climate spaces in NAM than in their native regions. Therefore, most of the 3021 species still have an enormous potential to spread further, as shown by the unused climate space available. However, the climate spaces used by the exotic plants were unbalanced; that is, there was a more significant overlap between used climate space and available space where MAT and MAP were low. In other words, exotic plants used more climate space in relatively cooler and drier places, as indicated by the much larger climate space available at high-maximum space than at minimum-low space (Fig. 5a b).

One of the stable and frequently used life history traits, seed size (weight, g), showed negative relationships with global native range size (Fig. 6a) and NAM exotic range (Fig. 6b) size as expected (partly due to the seed size-seed number trade-offs and greater dispersibility of smaller seeds than larger seeds) but an unexpected positive relationship with global exotic range size and no relationship with global native and exotic range size (Fig. 6c and d).

4. Discussion

Our findings show the future spread potentials of many introduced species in terms of climate space still available in their exotic regions. The minimum MATs across some exotic plants' ranges in NAM seem already reaching or exceeding their limits, although the southern part of NAM has higher exotic richness. The 3021 exotic species now occupy only a narrow range of potential precipitation gradients (MAP; Fig. 4). The spreads of the exotic plants are not even, with most climate space occupied where MAP is around 1000 mm (or 500−1500 mm) and MAT between -15 and 25 °C (Figs. 3 and 4). NAM lacks some warmer/drier climates that native regions have (as indicated by the blue symbols in Fig. 4; see also Fig. S5), which could limit the spread of certain species. However, this could only be the case if no significant genetic modification or adaptation occurs (Whitney and Gabler, 2008). Conversely, NAM also offers novel conditions for many introduced species with limited distributions, as shown in Figs. 1 and 4, especially if these species are not limited by climates in their native regions. Despite the considerable evidence for the "niche conservatism hypothesis" (Petitpierre et al., 2012), many also show 'niche shifts' after introduction, especially when all exotic regions are considered (Atwater et al., 2018).

The performance of nonnative plants in NAM that also occur in other parts of the world can better predict their distributions in NAM than their native distributions, suggesting that such introduced plants may perform more similarly among exotic regions than between native and exotic regions. This finding provides critical information needed for developing early warning systems. For example, NAM should enforce early actions to prevent the introduction of invasives that are successful in the rest of the world, and climate space is available in NAM (Early et al., 2016; Kendig et al., 2022). Conversely, our findings also provide insights into further invasion potential by introduced species in NAM with potential applications to other regions in the world. This is important because many species have already had much larger ranges in NAM than in their native regions. This may be partly due to the availability of more climate space in NAM and partly through enemy release (Liu and Stiling, 2006), mutualistic interactions (with native and even other exotic plants or animals) (Simberloff and Von Holle, 1999), and genetic adaptation and modification (Whitney and Gabler, 2008), among others.

The success of numerous invasive species around the world proves that many species may be the result of releasing from
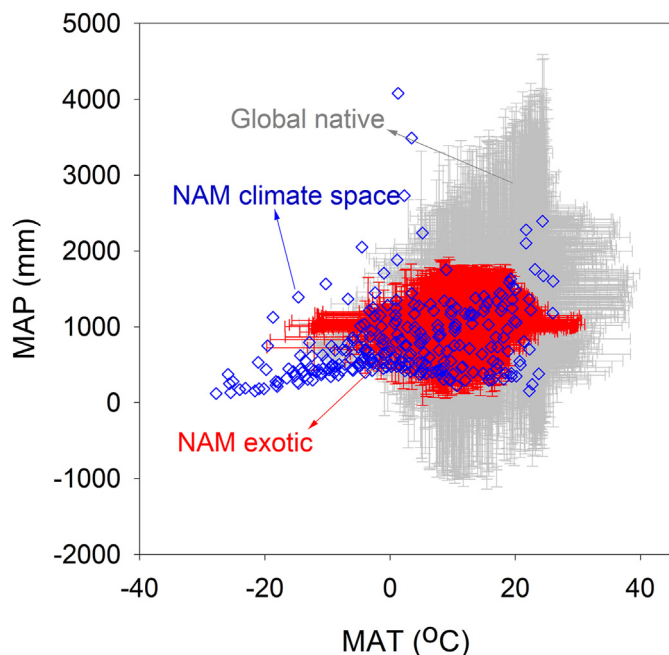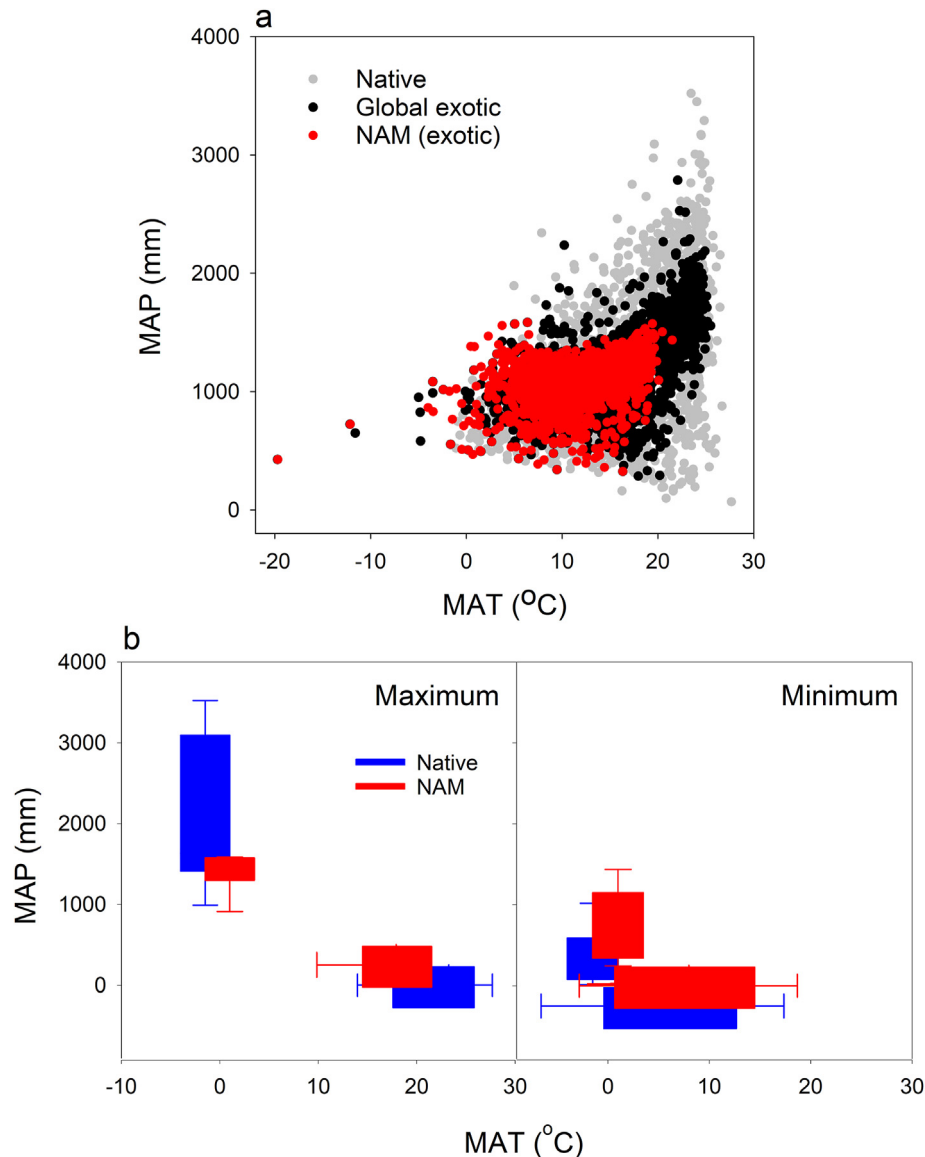
Fig. 5. The climate space used by the 3021 exotic plant species in their native and exotic regions. On average, the 3021 exotic species in North America north of Mexico (NAM) still occupy smaller climate spaces in NAM than in their native and other exotic (excluding NAM) regions around the world. (**a**) Most of the 3021 species introduced to NAM still have a large potential to spread further, as shown by unused climate space available, especially in warmer and wetter places, as indicated by the much more climate space available at high-maximum space than at minimum-low space. (**b**) A comparison of the minimum and maximum MAT and MAP used by the 3021 species in their native regions (blue) and in exotic NAM (red).

multiple biotic and abiotic constraints or stresses simultaneously, not just one factor at a time, such as natural enemies (Liu and Stiling, 2006). Our study shows that, in such a short period of time (i.e., only a few hundred years), many exotic plant species already have much larger ranges than their native ranges. This is particularly striking because our target exotic region, NAM, is vastly smaller than the rest of the globe as the native region of the 3021 species. This observation may have implications in predicting future species distribution based on their current distribution data used in available species distribution models or SDMs (or bioclimatic envelopes or ecological niche models) (Hui, 2023; Welk et al., 2002). The positive relationship between native and exotic range sizes of the same set of species (Fig. 2c) and a significant phylogenetic signal in the ratio of the exotic range sizes to the overall (i.e., native plus exotic) range sizes suggests that potential range sizes of newly naturalized species can to a certain extent be predicted both by their native range sizes and by exotic range sizes of their close relatives (Fig. 1).

It is not surprising that certain life history traits such as seed size can better explain native range sizes than exotic range sizes because many exotic species are still spreading (i.e., due to the time factor). [Unfortunately, for the vast majority of the 3021 species examined here, the time since invasions are still unknown because most of them were not intentionally introduced.] The opposite relationships between seed size and range size in global native plus exotic regions and global exotic regions may primarily be due to human intervention (e.g., it is possible humans might have intentionally introduced and spread large-seeded species for economic or some other purposes) (Petitpierre et al., 2012; Dong et al., 2023). A less frequently used but may be a more climate-sensitive trait, the photosynthetic pathways also reveal valuable information regarding species invasions. For example, while warmer
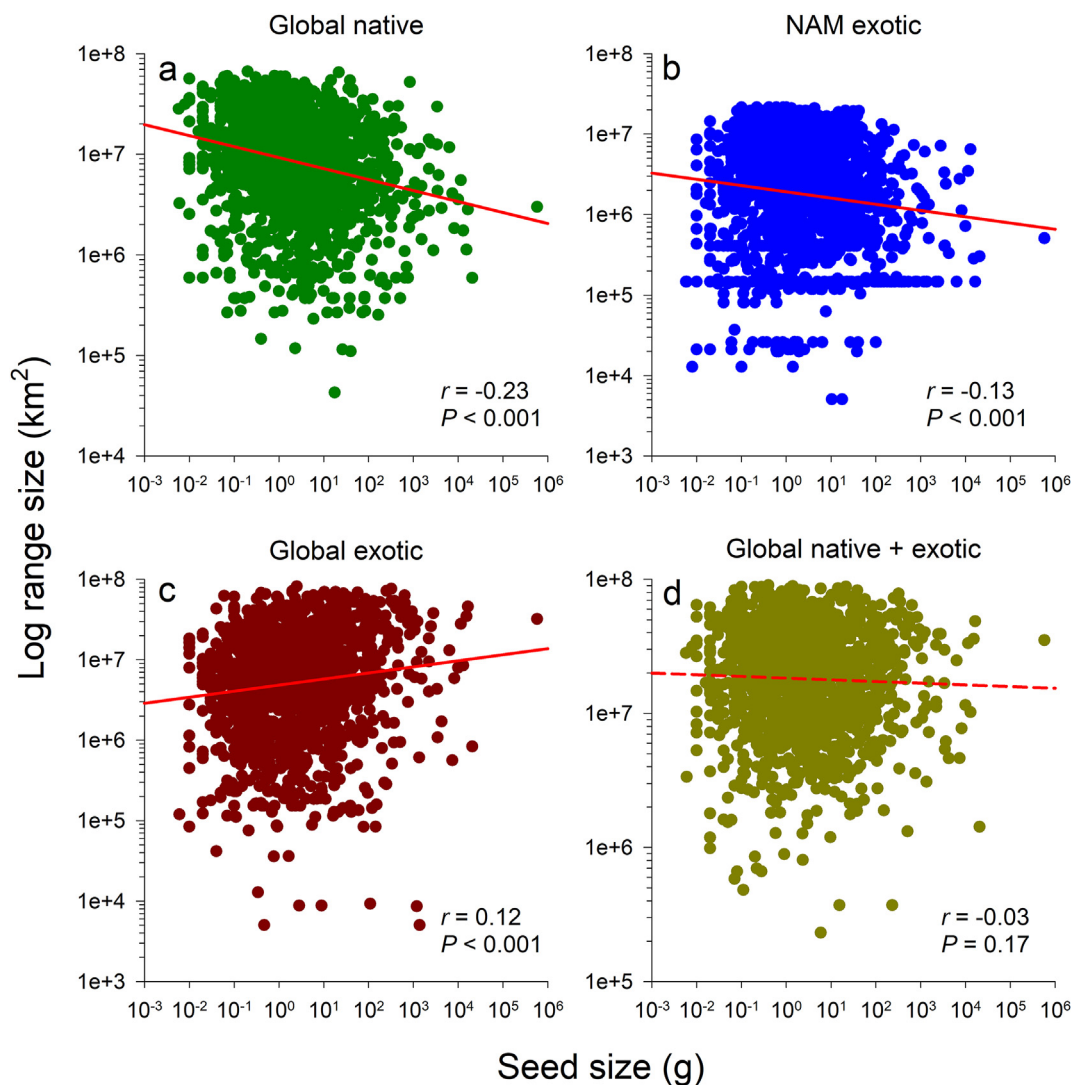
Fig. 6. Examples of life history traits (seed size) better explain native range sizes and exotic range sizes in NAM that are consistent with previous research. The opposite relationships between seed size and range size in global native plus exotic regions and in global exotic regions (including NAM) may be mostly due to human intervention (Petitpierre et al., 2012).

temperatures could potentially increase the productivity of C4 species, elevated atmospheric CO_2 may not promote photosynthesis in most C4 plants but could enhance the growth, yield, and abundance of C3 plants (Ehleringer and Monson, 1993; Hamilton III et al., 2008). This observation is consistent with the ongoing woody encroachment in NAM (Ratajczak et al., 2012).

Our findings from herbaceous vs. woody nonnative plant comparisons are consistent with previous observations on eastern Asia–North America disjunct plants that herbs show stronger relationships in range size between the two regions (Ricklefs and Latham, 1992; Liu et al., 2023). Herbaceous species considered here consistently have larger ranges in both native and exotic regions than woody species. More importantly, herbaceous species do show a stronger relationship in range size between native and exotic regions than woody species, further suggesting that the two groups of species have different ecological specializations and/or different sensitivities to similar environmental changes (Ricklefs and Latham, 1992; Smith and Beaulieu, 2009). It is possible that herbs could more rapidly fill in their potential niches than woody species because of their higher flexibility and adaptability, mostly due to their relatively shorter generation time (Smith and Beaulieu, 2009).

It is difficult to confirm to what extent the native distributions could be used to predict exotic distributions, at least in the NAM exotic plant case, where many exotic species are still spreading (many currently still have very small ranges in NAM relative to their native ranges) (see also Atwater et al., 2018). First, we only used MAT and MAP in both native and NAM as constraint climate variables to show spread potential. Yet, in the real world, other climate factors, such as persistent drought or extreme cold conditions, may be more critical for certain species (Petitpierre et al., 2012). Our study focused on MAT and MAP because many previous studies have shown that these two factors are major determinants of plant distributions (Whittaker, 1975). Second, although each species has a specific climate space, most species never fully use such space because of other important limiting factors such as dispersal, time to spread, land use, and interactions with coexisting species (e.g., as food sources or natural enemies). For these reasons, many species could only use part of their real climate niche. In addition, the spread of some species depends on future climate change that could directly or indirectly alter their niche availability and genetic adaptation (Bradley et al., 2010). Species shifting to higher latitudes after invasion may have larger and expanding ranges (e.g., Li et al.,

2014), which seems consistent with Rappoport's rule and the negative richness—range size relationship (that is, in species-rich regions at lower latitudes, species interact with more competitors or natural enemies) (Guo et al., 2022).

The applicability of the "niche conservatism hypothesis" in predicting species invasions could be influenced by two major factors: (1) time since invasion (whether species have had enough time to occupy their suitable habitats) (Williamson et al., 2009) and (2) how similar the regions (or source-recipient regions in species invasions) to be compared are (Qian and Ricklefs, 2004). Future research needs to identify what species are at the 'climatic equilibrium' with their environments and what species are far from it. It is highly possible that different range edges (e.g., margins at major cardinal directions at N, S, W, E) of the same species may be at different levels of climatic equilibrium or, in other words, part of range margins of the species may be limited by climate, but other margins may be confined by other factors. Furthermore, managed or human-assisted migration and species conservation could be more successful when the role of climate change and climate space is better understood for early planning and actions (Beaury et al., 2019).

In sum, our findings stress the importance of using species' distribution (rather than realized niche) in native regions to predict exotic or future distributions unless the native and target exotic regions are more or less comparable in size and environmental conditions (Guo et al., 2023). The levels of success in invasion in other parts of the world can better predict the distribution in NAM than the native distributions. Current distribution may often not indicate the range limits of most exotic but especially invasive species (Atwater et al., 2018). In the future, more studies are needed to examine whether different organisms show different levels of climatic control over species ranges. The answer to this question may be applied to management applications such as biocontrol (Tanga et al., 2021). For example, it is possible that dramatic climate change could cause the ranges (location and size) of more species to be limited by climate factors.

CRediT authorship contribution statement

Qinfeng Guo: Writing — original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Hong Qian:** Writing — review & editing, Methodology, Investigation, Formal analysis, Data curation. **Shenhua Qian:** Writing — review & editing, Investigation, Formal analysis, Data curation.

Data availability statement

The data used in this study have already been published, and the sources of the data were cited in the manuscript: i.e., http://onlinelibrary.wiley.com/doi/10.1002/ecy.2542/suppinfo, https://powo.science.kew.org/, https://www.newphytologist.org/global-plant-diversity, https://idata.idiv.de/DDM/Data/ShowData/257, https://chelsa-climate.org), https://plants.usda.gov/home, http://rs.tdwg.org/wgsrpd/doc/data/.

Declaration of competing interest

The authors have no competing interest to declare.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pld.2024.11.005.

References

Albright, T.P., Chen, H., Chen, L., et al., 2010. The ecological niche and reciprocal prediction of the disjunct distribution of an invasive species: the example of *Ailanthus altissima*. Biol. Invasions 12, 2413—2427.

Atwater, D.Z., Ervine, C., Barney, J.N., 2018. Climatic niche shifts are common in introduced plants. Nat. Ecol. Evol. 2, 34—43.

Beaury, E.M., Finn, J.T., Corbin, J.D., et al., 2019. Biotic resistance to invasion is ubiquitous across ecosystems of the United States. Ecol. Lett. 23, 476—482.

Blackburn, T.M., Pyšek, P., Bacher, S., et al., 2011. A proposed unified framework for biological invasions. Trends Ecol. Evol. 26, 333—339.

Bradley, B.A., Wilcove, D.S., Oppenheimer, M., 2010. Climate change increases risk of plant invasion in the Eastern United States. Biol. Invasions 12, 1855—1872.

Broennimann, O., Treier, U.A., Müller-Schärer, H., et al., 2007. Evidence of climatic niche shift during biological invasion. Ecol. Lett. 10, 701—709.

Brown, M.J., Walker, B.E., Black, N., et al., 2023. rWCVP: a companion R package for the world checklist of vascular plants. New Phytol. 240, 1355—1365.

Brummitt, R.K., 2001. World geographical scheme for recording plant distributions. Hunt Institute for Botanical Documentation, second ed. Carnegie Mellon University Press, Pittsburgh.

Casado, M.A., Martín-Forés, I., Castro, I., et al., 2018. Asymmetric flows and drivers of herbaceous plant invasion success among Mediterranean-climate regions. Sci. Rep. 8, 16834.

Dangles, O., Carpio, C., Barragan, A., et al., 2008. Temperature as a key driver of ecological sorting among invasive pest species in the tropical Andes. Ecol. Appl. 18, 1795—1809.

Dong, B.C., Yang, Q., Kinlock, N.L., et al., 2023. Naturalization of introduced plants is driven by life-form-dependent cultivation biases. Divers. Distrib. 30, 55—70.

Early, R., Bradley, B.A., Dukes, J.S., et al., 2016. Global threats from invasive alien species in the twenty-first century and national response capacities. Nat. Commun. 7, 12485.

Early, R., Sax, D.F., 2014. Climatic niche shifts between species' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change. Global Ecol. Biogeogr. 23, 1356—1365.

Ehleringer, J.R., Monson, R.K., 1993. Evolutionary and ecological aspects of photosynthetic pathway variation. Annu. Rev. Ecol. Syst. 24, 411—439.

Gallien, L., Münkemüller, T., Albert, C.H., et al., 2010. Predicting potential distributions of invasive species: where to go from here? Divers. Distrib. 16, 331—342.

Garcia, R.A., Araujo, M.B., Burgess, N.D., et al., 2014. Matching species traits to projected threats and opportunities from climate change. J. Biogeogr. 41, 724—735.

Gioria, M., Hulme, P.E., Richardson, D.M., et al., 2023. Why are invasive plants successful? Annu. Rev. Plant Biol. 74, 635—670.

Goodwin, B.J., McAllister, A.J., Fahrig, L., 1999. Predicting invasiveness of plant species based on biological information. Conserv. Biol. 13, 422—426.

Guo, Q., 2006. Intercontinental biotic invasions: what can we learn from native populations and habitats? Biol. Invasions 8, 1451—1459.

Guo, Q., Brown, J.H., Valone, T.J., et al., 2000. Constraints of seed size on plant distribution and abundance. Ecology 81, 2149—2155.

Guo, Q., Qian, H., Ricklefs, R.E., et al., 2006. Distributions of exotic plants in eastern Asia and North America. Ecol. Lett. 9, 827—834.

Guo, Q., Qian, H., Zhang, J., 2022. On the relationship between species diversity and range size. J. Biogeogr. 49, 1911—1919.

Guo, Q., Qian, H., Zhang, J., 2023. Does regional species diversity resist biotic invasions? Plant Divers. 45, 353—357.

Guo, Q., Sax, D.F., Qian, H., et al., 2012. Latitudinal shifts of introduced species: possible causes and implications. Biol. Invasions 14, 547—556.

Hamilton III, E.W., Heckathorn, S.A., Joshi, P., et al., 2008. Interactive effects of elevated CO_2 and growth temperature on the tolerance of photosynthesis to acute heat stress in C3 and C4 species. J. Integr. Plant Biol. 50, 1375—1387.

Hock, M., Hofmann, R., Essl, F., et al., 2020. Native distribution characteristics rather than functional traits explain preadaptation of invasive species to high-UV-B environments. Divers. Distrib. 26, 1421—1438.

Hui, C., 2023. The dos and don'ts for predicting invasion dynamics with species distribution models. Biol. Invasions 25, 947—953.

Jandt, U., Sporbert, M., Welk, E., et al., 2021. Different sets of traits explain abundance and distribution patterns of European plants at different spatial scales. J. Veg. Sci. 32, e13016.

Jia, J., Dai, Z., Li, F., et al., 2016. How will global environmental changes affect the growth of alien plants? Front. Plant Sci. 7, 1623.

Jin, Y., Qian, H., 2023. U.PhyloMaker: an R package that can generate large phylogenetic trees for plants and animals. Plant Divers. 45, 347—352.

Karger, D.N., Conrad, O., Böhner, J., et al., 2017. Climatologies at high resolution for the earth's land surface areas. Sci. Data 4, 1—20.

Kembel, S.W., Cowan, P.D., Helmus, M.R., et al., 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26, 1463—1464.

Kendig, A.E., Canavan, S., Anderson, P.J., et al., 2022. Scanning the horizon for invasive plant threats using a data-driven approach. NeoBiota 74, 129—154.

Liu, H., Stiling, P., 2006. Testing the enemy release hypothesis: a review and meta-analysis. Biol. Invasions 8, 1535—1545.

Liu, Y., Heberling, J.M., Wang, Z., et al., 2023. Niche unfilling dominates the naturalization of species from intercontinentally disjunct genera. Global Ecol. Biogeogr. 32, 1977—1990.

McLachlan, J.S., Hellmann, J.J., Schwartz, M.W., 2007. A framework for debate of assisted migration in an era of climate change. Conserv. Biol. 21, 297—302.

Nunez-Mir, G.C., Guo, Q., Rejmánek, M., et al., 2019. Predicting invasiveness of exotic woody species using a traits-based framework. Ecology 100, e02797.

Pagel, M., 1999. Inferring the historical patterns of biological evolution. Nature 401, 877—884.

Pearson, D.E., Clark, T.J., Hahn, P.G., 2022. Evaluating unintended consequences of intentional species introductions and eradications for improved conservation management. Conserv. Biol. 36, e13734.

Petitpierre, B., Kueffer, C., Broennimann, O., et al., 2012. Climatic niche shifts are rare among terrestrial plant invaders. Science 335, 1344—1348.

Pyšek, Pergl, J., Essl, F., et al., 2017. Naturalized alien flora of the world: species diversity, taxonomic and phylogenetic patterns, geographic distribution and global hotspots of plant invasion. Preslia 89, 203—274.

Pyšek, P., 1998. Is there a taxonomic pattern to plant invasions? Oikos 82, 282—294.

Qian, H., 2023a. Global patterns of phylogenetic relatedness of invasive flowering plants. Divers. Distrib. 29, 1106—1117.

Qian, H., 2023b. Intercontinental comparison of phylogenetic relatedness in introduced plants at the transition from naturalization to invasion: a case study on the floras of South Africa and China. Plant Divers. 45, 363—368.

Qian, H., 2023c. Patterns of phylogenetic relatedness of non-native plants across the introduction—naturalization—invasion continuum in China. Plant Divers. 45, 169—176.

Qian, H., Deng, T., 2024. Species invasion and phylogenetic relatedness of vascular plants on the Qinghai-Tibet Plateau, the roof of the world. Plant Divers. https://doi.org/10.1016/j.pld.2023.01.001.

Qian, H., Rejmánek, M., Qian, S., 2022. Are invasive species a phylogenetically clustered subset of naturalized species in regional floras? A case study for flowering plants in China. Divers. Distrib. 28, 2084—2093.

Qian, H., Ricklefs, R.E., 2004. Geographical distribution and ecological conservatism of disjunct genera of vascular plants in eastern Asia and eastern North America. J. Ecol. 92, 253—265.

Ratajczak, Z., Nippert, J.B., Collins, S.L., 2012. Woody encroachment decreases diversity across North American grasslands and savannas. Ecology 93, 697—703.

Reichard, S.H., Hamilton, C.W., 1997. Predicting invasions of woody plants introduced into North America. Conserv. Biol. 11, 193—203.

Rejmánek, M., 2014. Invasive trees and shrubs: where do they come from and what we should expect in the future? Biol. Invasions 16, 483—498.

Rejmánek, M., Richardson, D.M., 1996. What attributes make some plant species more invasive? Ecology 77, 1655—1661.

Richardson, D., Williams, P., Hobbs, R.J., 1994. Pine invasions in the Southern Hemisphere: determinants of spread and invadability. J. Biogeogr. 21, 511—527.

Richardson, D.M., Pyšek, P., 2012. Naturalization of introduced plants: ecological drivers of biogeographical patterns. New Phytol. 196, 383—396.

Ricklefs, R.E., Guo, Q., Qian, H., 2008. Growth form and distribution of introduced plants in their native and non-native ranges in Eastern Asia and North America. Divers. Distrib. 14, 381—386.

Ricklefs, R.E., Latham, R.E., 1992. Intercontinental correlation of geographical ranges suggests stasis in ecological traits of relict genera of temperate perennial herbs. Am. Nat. 139, 1305—1321.

Simberloff, D., Von Holle, B., 1999. Positive interactions of nonindigenous species: invasional meltdown? Biol. Invasions 1, 21—32.

Smith, S.A., Beaulieu, J.M., 2009. Life history influences rates of climatic niche evolution in flowering plants. Proc. Royal Soc. B-Biol. Sci. 276, 4345—4352.

Sychrová, M., Divíšek, J., Chytrý, M., et al., 2022. Niche and geographical expansions of North American trees and tall shrubs in Europe. J. Biogeogr. 49, 1151—1161.

Tanga, C.M., Ghemoh, C.J., Tonnang, H.E., et al., 2021. Eco-climatic matching to guide foreign exploration and optimal release strategies for biological control agents of *Rastrococcus iceryoides* in Africa and Asia. Biol. Control 158, 104603.

Thomas, C.D., 2010. Climate, climate change and range boundaries. Divers. Distrib. 16, 488—495.

van Kleunen, M., Dawson, W., Essl, F., et al., 2015. Global exchange and accumulation of non-native plants. Nature 525, 100—103.

van Kleunen, M., Pyšek, P., Dawson, W., et al., 2019. The global naturalized alien flora (Glo NAF) database. Ecology 100, e02542.

Welk, E., Schubert, K., Hoffmann, M.H., 2002. Present and potential distribution of invasive garlic mustard (*Alliaria petiolata*) in North America. Divers. Distrib. 8, 219—233.

Whitney, K.D., Gabler, C.A., 2008. Rapid evolution in introduced species,'invasive traits' and recipient communities: challenges for predicting invasive potential. Divers. Distrib. 14, 569—580.

Whittaker, R.H., 1975. Communities and Ecosystems. Macmillan, New York.

Williamson, M., Dehnen-Schmutz, K., Kühn, I., et al., 2009. The distribution of range sizes of native and alien plants in four European countries and the effects of residence time. Divers. Distrib. 15, 158—166.

Zhang, J., Qian, H., 2023. U.Taxonstand: an R package for standardizing scientific names of plants and animals. Plant Divers. 45, 1—5.

Zhang, Z., Yang, Q., Fristoe, T.S., et al., 2023. The poleward naturalization of intra-continental alien plants. Sci. Adv. 9, eadi1897.