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Climatic niche shifts are rare among terrestrial plant invaders

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Using distribution data for 50 species across Eurasia, North America and Australia, we show that invasive terrestrial plant species rarely expand their climatic niche in their invaded ranges.

The assumption that climatic niche requirements of invasive species are conserved between their native and invaded ranges is key to predicting the risk of invasion. However, this assumption has been challenged recently by evidence of niche shifts in some species. Here, we report the first large-scale test of niche conservatism for 50 terrestrial plant invaders between Eurasia, North America and Australia. We show
that when analog climates are compared between regions, fewer than 15% of species have more than 10% of their invaded distribution outside their native climatic niche. These findings reveal that significant niche shifts are rare in terrestrial plant invaders, providing new support for an appropriate use of ecological niche models for the prediction of both biological invasions and responses to climate change.

Niche conservatism in space and time is a key assumption for predicting the impact of global change on biodiversity (1, 2). It is particularly important for the anticipation of biological invasions, which can cause severe damage to biodiversity, economies and human health (3). Niche conservatism implies that species tend to grow and survive under the same environmental conditions in native and invaded ranges (2). However, the generality of this assumption is challenged by recent evidence suggesting that the climatic niche occupied by species may not be conserved between their native and invaded ranges, as documented by observed niche shifts for plants (4, 5), insects (6, 7) and fishes (8). Yet, several of these studies have focused on a single species (e.g. 4, 6, 7) or have used controversial niche overlap metrics (e.g. 5, 8; based on 26 and 18 spp respectively), making it difficult to assess the generality of this phenomenon among alien invasive species. Therefore, the question of whether niche shifts represent a prominent or unusual phenomenon among alien invasive species remains largely unresolved (9).

There are two major reasons why niche conservatism during biological invasion needs further investigation. First, anticipation is the most effective management strategy (10) and niche conservatism is a strong and necessary assumption to predict invasion risk for specific regions (1, 2). Ecological niche models (ENM, 11, 12), the most commonly used
predictive tool in this regard, are traditionally calibrated using native species distributions and then projected onto other continents to highlight areas susceptible to invasions (13). Second, detecting significant deviations from niche conservatism may highlight invasive species that are characterized by ecological (14, 15) or evolutionary changes (16, 17) during invasions, helping us understand when such changes are likely to occur, which is crucial in an era of rapid climate change.

When the niche of a species changes, its mean position (centroid) is likely to move within a multivariate environmental niche space. However, describing the shift of the centroid (4, 5, 7) falls short in helping to understand processes affecting the niche, because niche changes can affect both the position and the shape of a niche. This is for example, the case when species expand to new climates at one particular niche margin (1, 4) and only partially fill the niche (i.e. unfilling) at another (18) (e.g., due to dispersal limitation) (Fig. S1). Assuming a species is at equilibrium in its native range (i.e., has colonized all suitable environments), then expansion to climates that are new to the species but available in the native range should be considered unambiguously as niche shifts (12, Fig. S1), i.e., resulting from changes in biotic interactions or rapid evolution of the species (1). This conceptual approach to detecting niche shifts is important because analyses of empirical field data alone cannot determine whether the expansion to climates not available in the native range (i.e., non-analog climates) represents a true niche shift or the filling of a pre-adapted niche. On the other hand, unfilling in the invaded range is more likely due to dispersal limitation, because biological invasions are recent and ongoing phenomena.
Niche changes due to unfilling have been considered niche shifts in previous studies (4-7) but our analyses (12) reveal that many of these reflect ongoing colonization instead, indicating that the species is likely to invade additional geographic regions in the future (13). Thus, metrics of niche shift are very sensitive to the underlying statistical and conceptual assumptions and a solid conceptual foundation for identifying ecologically meaningful and statistically significant niche changes has only recently been developed (12, 19-21).

Here, we disentangle and quantify the amount of niche overlap, niche expansion and niche unfilling (see Fig. S1 and S2) for 50 Holarctic terrestrial alien angiosperms (Tables S1 and S2). Plants are appropriate for this test because their distributions are largely limited by climatic factors (22), a necessary condition to assess niche conservatism. Our sample includes many of the major plant invaders between North America (NA) and Eurasia (EU) and also many of the most anciently introduced EU species in NA. The reciprocal comparison of EU and NA invaders provides an important test of niche conservatism because it is the only pair of two large, separated landmasses with a largely overlapping climate space and a long history of reciprocal anthropogenic exchanges of floras (23, 24). When available, the distribution of these species in Australia (AU, Table S3), where none is native, was used to provide additional, independent insights into patterns of niche filling when climatic availability, although partly overlapping, is overall very different from the native range. Geographical distributions (resolution = 0.5°, approximately 50 km) were projected onto climate space following a niche quantification framework correcting for species densities and climatic availability in both the native and invaded range (12, 21). This approach tests for niche conservatism and robustly quantifies the amount of niche overlap, expansion and unfilling in the invaded range.
We find little evidence of niche expansion associated with invasion of new regions. Our results for the Holarctic reveal that, although levels of niche overlap among species vary between 17% and 64% (Fig. 1, Table S5), niche conservatism is observed for 46% of species (23) between the native and invaded range in EU and NA (similarity test with a significance level ≤ 0.05; Fig. 1, Table S5). NA species show higher propensity toward niche similarity (13 out of 20 species). In contrast to comparisons between EU and NA, niche similarity tests for Australia are significant for all species (Table S6) despite more pronounced climatic differences between AU and both EU and NA, respectively, than between EU and NA. This indicates that in AU, Holarctic invasive species remain in Holarctic climates and are rarely found in new climates. In other words, when considering the available climate in the invaded range, species colonize climatic conditions close to the ones colonized in their native range.

Further differentiating non-overlap situations into cases of unfilling or expansion reveals that in the Holarctic only 14% of the studied species (7) show more than 10% expansion, with only one outlier species - spotted knapweed (*Centaurea stoebe*) - showing >50% expansion (Fig. 1, Fig. 2, Table S5). Previous studies also reported an important niche shift for this species (4), possibly caused by evolutionary (25) and/or ecological processes (15), notably through hybridization (4, 26,) and enhanced competitive strength in the invaded range (27). Interestingly, there is also evidence of novel genetic admixing (repeated introductions or hybridization) and reduced impacts of competitors and enemies in many of the other studied species (e.g., 26, 28-30) but these species did not show any major niche expansion, indicating that these mechanisms do not necessarily lead to niche expansion. Indeed, niche unfilling is a more widespread phenomenon with 48% of
species (24) showing more than 10% of their native niche unfilled in the invasive range (Fig. 1 and Fig. 3). Patterns in Australia confirm these Holarctic findings, i.e., niche expansion is uncommon compared to unfilling (Fig. 2, Fig. 4, Fig. S4, Table S6).

The biogeographical origin of the species provides further insights into niche comparisons between native and invaded ranges (Fig. 3 and Fig. 4). In general, EU species show less niche unfilling and more expansion in NA and AU than NA species in EU and AU, thus mirroring biogeographical patterns of invasibility, which show higher invasion rates of NA compared to EU (31). Differences in the geographic arrangement of EU versus NA could account for the difference in niche unfilling. In particular, climate varies on a shorter distance along latitudinal gradients in NA than EU and may allow more rapid expansion into different climates in NA (32). However, this does not explain why EU species also show less niche unfilling in AU than NA species. Biome conservatism, frequent across long evolutionary time scales (33) and highly expected in the case of invasive species (13), may further explain niche differences between areas differing in biome availability (Fig. 3 and Fig. 4). In NA and AU, EU species expansions occur toward hotter and drier niche limits, corresponding in NA to the median climatic conditions of temperate coniferous forests, which are mostly absent in EU (Fig. 3). The lower prevalence of niche unfilling in EU species may relate to the longer history of weed selection in human-disturbed landscapes in Europe and earlier colonization paths from Europe to other continents (23, 24). However, when testing the effect of minimum residence time on niche expansion, overlap, unfilling and total change magnitude, we found no significant effect (Table S5), suggesting that other drivers, such as human-mediated propagule pressure, likely prevail. Movement of human settlements was far more important from EU towards NA and AU than the opposite (31), as shown by higher
numbers of Eurasian invaders worldwide (24) and this could explain less unfilling among EU species.

Our findings have implications for anticipating biological invasions. They suggest that ENMs remain reasonable tools to predict invasions from the native range if study areas have comparable environments, at least with regard to the biologically relevant variables. This was indeed the rule in most of our species and thus is likely to also apply to many other terrestrial alien invasive plants. To illustrate this, we built ENM for each species’ native distribution. The models reveal on average a fair transferability, with only a minority of poor predictions in the invaded range (8 NA species and 2 EU species) based on the Boyce index (B; 12). As expected, we found a positive correlation between B and the niche overlap D, and negative correlations between B and total niche changes (Fig. S6). Interestingly, similar results are obtained when comparing niche metrics with ENM predictions calibrated on the analog climates between EU and NA or on the whole climate (Fig. S7). Using the approach to niche comparison (21) as a complement to ENMs thus remains important because it allows disentangling of disequilibrium situations, such as niche expansion or partial filling, in analog climates (Fig. 1).

Our findings that climatic niche shifts are rare among terrestrial plant invaders between their native and introduced ranges parallels results from a recent study showing that increase in species’ abundance are rare between ranges (34). We found only a few plant invaders (e.g., spotted knapweed) showing an important proportion of their invaded range outside their native niche, possibly resulting from ecological and/or evolutionary changes, although we cannot exclude dispersal limitation in the native range as a possible contributing factor. Conversely, most reported niche differences are likely caused by
Recognizing that some cases of true niche change do exist, further assessments should seek to understand strategies that have allowed these particular alien invasive species to expand their niches dramatically, with possible implications for biocontrol (35). Although our study focused on Holarctic plant invaders, they included a wide range of plants, ranging from trees to herbs. It would be particularly interesting to use the same framework to test whether the same pattern is found in other organisms, especially in aquatic plants, as some of these are known to have a very large invaded range compared to their native one (36). Finally, our study specifically tested for niche change between geographic regions, but our general finding of niche conservation also supports an important role for ENMs in assessments of species vulnerability to climate change over time (I).

\References


12. Materials and methods are available as supporting material on Science Online.


**Supporting Online Material**

www.sciencemag.org

Materials and Methods

SOM Text

Figures S1-S10

Tables S1-S9

References (37-64)

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study are available online. Species data used in this study were assembled from multiple sources with various release politics. All data sources are described in the SOM.

\Figure legends

**Fig.1. Niche changes between native and invaded ranges in Eurasia (EU) and North America (NA).** Vertical segments represent the magnitude of niche changes for each species. Extensions above and below the zero plane indicate expansion and unfilling, respectively. Intersections with the zero plane are shown with dots. Green (EU) and red (NA) colors indicate species origin. Niche change indices are plotted over two niche overlap indices, Schoener’s D and the Boyce index evaluation of ecological niche models (ENM) calibrated in the native range and projected onto analog climates in the invaded range. Stars show species with a significant niche overlap between native and invaded range based on a similarity test.

**Fig.2. Expansion in Holarctic and Australian invaded ranges.** The expansion index is analogous to the proportion of the invasive distribution in novel environments. NA and EU species origins are shown with red and green colors respectively.

**Fig. 3. Niche dynamic between native and invaded ranges in Holarctic environmental space** depicted by the first two axes of a principal component analysis, calibrated on the entire range of conditions available in NA (red contour lines) and EU (green contour lines). Niche expansion, overlap and unfilling situations are stacked in the environmental space for each species. Bidimensional color keys represent the number of
species showing expansion (grey to red, A), unfilling (grey to green, B) and overlap (grey to blue, A and B). Occupied color classes are shown by black dots. C represents the distribution of biomes in the invaded environmental space.

**Fig. 4. Niche dynamic between native and invaded ranges in Australian environmental space.** Same legend as Fig. 3, except realized environment in AU is additionally represented (blue contour lines) and C represents biomes distribution in AU.

**Fig. 1**

![Graph showing niche dynamics between native and invaded ranges in Australian environmental space.](image)

| 1. Acer negundo | 18. Cytisus scoparius | 35. Plantago major* |
| 5. Amygdalus fruticosa | 22. Eryngium annua* | 39. Rhus hirta* |
| 7. Anthoxanthum odoratum* | 24. Euphorbia esula | 41. Rudbeckia laciniata* |
| 8. Arabidopsis thaliana* | 25. Helianthus tuberosus | 42. Rumex acetosella |
| 10. Aster novi-belgii* | 27. Hypochaeris radicata | 44. Solidago gigantea* |
| 13. Bromus tectorum* | 30. Lythrum salicaria* | 47. Trifolium dubium* |
| 15. Centaurea stoebe | 32. Melilotus albus | 49. Verbascum thapsus |
| 16. Cirsium vulgare | 33. Phytolacca americana* | 50. Vicia sativa* |
| 17. Cytisus scoparius | 34. Plantago lanceolata |   

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Fig. 2

![Graph showing the number of species in the Arctic invaded range and the Australian invaded range.](image-url)
Fig. 3

**Biome legend**
- Tropical & subtropical moist broadleaf forest
- Tropical & subtropical dry broadleaf forest
- Tropical & subtropical coniferous forest
- Temperate broadleaf & mixed forest
- Temperate conifer forest
- Boreal forest/taiga
- Tropical & subtropical grassland, savanna & shrubland
- Temperate grassland, savanna & shrubland
- Flooded grassland, savanna & shrubland
- Montane grassland & shrubland
- Tundra
- Mediterranean forest, woodland & scrub
- Desert & xeric forest, woodland & shrubland