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1 **\Report**

2 \Title

3 Climatic niche shifts are rare among terrestrial plant invaders

4

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14

15 \Sentence summary

16 Using distribution data for 50 species across Eurasia, North America and Australia, we

17 show that invasive terrestrial plant species rarely expand their climatic niche in their

18 invaded ranges.

19

20 \Abstract

21 **The assumption that climatic niche requirements of invasive species are conserved**

22 **between their native and invaded ranges is key to predicting the risk of invasion.**

23 **However, this assumption has been challenged recently by evidence of niche shifts in**

24 **some species. Here, we report the first large-scale test of niche conservatism for 50**

25 **terrestrial plant invaders between Eurasia, North America and Australia. We show**

26 **that when analog climates are compared between regions, fewer than 15% of species**
27 **have more than 10% of their invaded distribution outside their native climatic**
28 **niche. These findings reveal that significant niche shifts are rare in terrestrial plant**
29 **invaders, providing new support for an appropriate use of ecological niche models**
30 **for the prediction of both biological invasions and responses to climate change.**

31

32 \Text

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

46

47 There are two major reasons why niche conservatism during biological invasion needs
48 further investigation. First, anticipation is the most effective management strategy (10)
49 and niche conservatism is a strong and necessary assumption to predict invasion risk for
50 specific regions (1, 2). Ecological niche models (ENM, 11, 12), the most commonly used

51 predictive tool in this regard, are traditionally calibrated using native species distributions
52 and then projected onto other continents to highlight areas susceptible to invasions (13).
53 Second, detecting significant deviations from niche conservatism may highlight invasive
54 species that are characterized by ecological (14, 15) or evolutionary changes (16, 17)
55 during invasions, helping us understand when such changes are likely to occur, which is
56 crucial in an era of rapid climate change.

57

58 When the niche of a species changes, its mean position (centroid) is likely to move within
59 a multivariate environmental niche space. However, describing the shift of the centroid
60 (4, 5, 7) falls short in helping to understand processes affecting the niche, because niche
61 changes can affect both the position and the shape of a niche. This is for example, the
62 case when species expand to new climates at one particular niche margin (1, 4) and only
63 partially fill the niche (i.e. unfilling) at another (18) (e.g., due to dispersal limitation)
64 (Fig. S1). Assuming a species is at equilibrium in its native range (i.e., has colonized all
65 suitable environments), then expansion to climates that are new to the species but
66 available in the native range should be considered unambiguously as niche shifts (12, Fig.
67 S1), i.e., resulting from changes in biotic interactions or rapid evolution of the species (1).
68 This conceptual approach to detecting niche shifts is important because analyses of
69 empirical field data alone cannot determine whether the expansion to climates not
70 available in the native range (i.e., non-analog climates) represents a true niche shift or the
71 filling of a pre-adapted niche. On the other hand, unfilling in the invaded range is more
72 likely due to dispersal limitation, because biological invasions are recent and ongoing
73 phenomena.

74

75 Niche changes due to unfilling have been considered niche shifts in previous studies (4-7)
76 but our analyses (12) reveal that many of these reflect ongoing colonization instead,
77 indicating that the species is likely to invade additional geographic regions in the future
78 (13). Thus, metrics of niche shift are very sensitive to the underlying statistical and
79 conceptual assumptions and a solid conceptual foundation for identifying ecologically
80 meaningful and statistically significant niche changes has only recently been developed
81 (12, 19-21).

82

83 Here, we disentangle and quantify the amount of niche overlap, niche expansion and
84 niche unfilling (see Fig. S1 and S2) for 50 Holarctic terrestrial alien angiosperms (Tables
85 S1 and S2). Plants are appropriate for this test because their distributions are largely
86 limited by climatic factors (22), a necessary condition to assess niche conservatism. Our
87 sample includes many of the major plant invaders between North America (NA) and
88 Eurasia (EU) and also many of the most anciently introduced EU species in NA. The
89 reciprocal comparison of EU and NA invaders provides an important test of niche
90 conservatism because it is the only pair of two large, separated landmasses with a largely
91 overlapping climate space and a long history of reciprocal anthropogenic exchanges of
92 floras (23, 24). When available, the distribution of these species in Australia (AU, Table
93 S3), where none is native, was used to provide additional, independent insights into
94 patterns of niche filling when climatic availability, although partly overlapping, is overall
95 very different from the native range. Geographical distributions (resolution = 0.5°,
96 approximately 50 km) were projected onto climate space following a niche quantification
97 framework correcting for species densities and climatic availability in both the native and
98 invaded range (12, 21). This approach tests for niche conservatism and robustly
99 quantifies the amount of niche overlap, expansion and unfilling in the invaded range.

100

101 We find little evidence of niche expansion associated with invasion of new regions. Our
102 results for the Holarctic reveal that, although levels of niche overlap among species vary
103 between 17% and 64% (Fig. 1, Table S5), niche conservatism is observed for 46% of
104 species (23) between the native and invaded range in EU and NA (similarity test with a
105 significance level ≤ 0.05 ; Fig. 1, Table S5). NA species show higher propensity toward
106 niche similarity (13 out of 20 species). In contrast to comparisons between EU and NA,
107 niche similarity tests for Australia are significant for all species (Table S6) despite more
108 pronounced climatic differences between AU and both EU and NA, respectively, than
109 between EU and NA. This indicates that in AU, Holarctic invasive species remain in
110 Holarctic climates and are rarely found in new climates. In other words, when
111 considering the available climate in the invaded range, species colonize climatic
112 conditions close to the ones colonized in their native range.

113

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

125 species (24) showing more than 10% of their native niche unfilled in the invasive range
126 (Fig. 1 and Fig. 3). Patterns in Australia confirm these Holarctic findings, i.e., niche
127 expansion is uncommon compared to unfilling (Fig. 2, Fig. 4, Fig. S4, Table S6).

128

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

150 numbers of Eurasian invaders worldwide (24) and this could explain less unfilling among
151 EU species.

152

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

167

168 Our findings that climatic niche shifts are rare among terrestrial plant invaders between
169 their native and introduced ranges parallels results from a recent study showing that
170 increase in species' abundance are rare between ranges (34). We found only a few plant
171 invaders (e.g., spotted knapweed) showing an important proportion of their invaded range
172 outside their native niche, possibly resulting from ecological and/or evolutionary
173 changes, although we cannot exclude dispersal limitation in the native range as a possible
174 contributing factor. Conversely, most reported niche differences are likely caused by

175 partial filling of the native niche in the invaded range. Recognizing that some cases of
176 true niche change do exist, further assessments should seek to understand strategies that
177 have allowed these particular alien invasive species to expand their niches dramatically,
178 with possible implications for biocontrol (35). Although our study focused on Holarctic
179 plant invaders, they included a wide range of plants, ranging from trees to herbs. It would
180 be particularly interesting to use the same framework to test whether the same pattern is
181 found in other organisms, especially in aquatic plants, as some of these are known to have
182 a very large invaded range compared to their native one (36). Finally, our study
183 specifically tested for niche change between geographic regions, but our general finding
184 of niche conservatism also supports an important role for ENMs in assessments of species
185 vulnerability to climate change over time (1).

186

187

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276 **Supporting Online Material**

278 www.sciencemag.org

279 Materials and Methods

280 SOM Text

281 Figures S1-S10

282 Tables S1-S9

283 References (37-64)

284

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

294

295

296 \Figure legends

297

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

307

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

311

312 **Fig. 3. Niche dynamic between native and invaded ranges in Holarctic**
313 **environmental space** depicted by the first two axes of a principal component analysis,
314 calibrated on the entire range of conditions available in NA (red contour lines) and EU
315 (green contour lines). Niche expansion, overlap and unfilling situations are stacked in the
316 environmental space for each species. Bidimensional color keys represent the number of

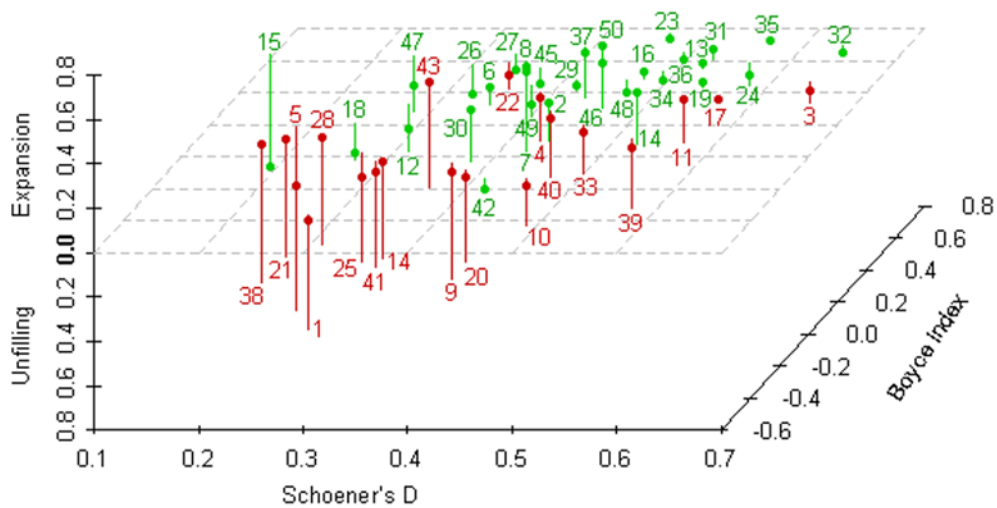
317 species showing expansion (grey to red, A), unfilling (grey to green, B) and overlap (grey
 318 to blue, A and B). Occupied color classes are shown by black dots. C represents the
 319 distribution of biomes in the invaded environmental space.

320

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

324

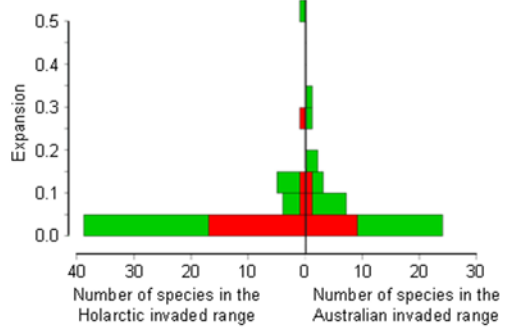
325 Fig. 1



1 <i>Acer negundo</i>	18 <i>Cytisus scoparius</i>	35 <i>Plantago major*</i>
2 <i>Alliaria petiolata*</i>	19 <i>Dactylis glomerata</i>	36 <i>Poa annua</i>
3 <i>Amaranthus retroflexus</i>	20 <i>Echinocystis lobata</i>	37 <i>Potentilla recta</i>
4 <i>Ambrosia artemisiifolia*</i>	21 <i>Epilobium ciliatum</i>	38 <i>Prunus serotina</i>
5 <i>Amorpha fruticosa</i>	22 <i>Erigeron annuus*</i>	39 <i>Rhus hirta*</i>
6 <i>Anagallis arvensis*</i>	23 <i>Erodium cicutarium</i>	40 <i>Robinia pseudoacacia</i>
7 <i>Anthoxanthum odoratum*</i>	24 <i>Euphorbia esula</i>	41 <i>Rudbeckia laciniata*</i>
8 <i>Arabidopsis thaliana*</i>	25 <i>Helianthus tuberosus</i>	42 <i>Rumex acetosella</i>
9 <i>Asclepias syriaca*</i>	26 <i>Holcus lanatus</i>	43 <i>Solidago canadensis*</i>
10 <i>Aster novi-belgii*</i>	27 <i>Hypochaeris radicata</i>	44 <i>Solidago gigantea*</i>
11 <i>Bidens frondosa*</i>	28 <i>Juncus tenuis*</i>	45 <i>Sonchus oleraceus</i>
12 <i>Bromus sterilis</i>	29 <i>Linaria vulgaris</i>	46 <i>Trifolium arvense</i>
13 <i>Bromus tectorum*</i>	30 <i>Lythrum salicaria*</i>	47 <i>Trifolium dubium*</i>
14 <i>Carduus nutans</i>	31 <i>Medicago lupulina</i>	48 <i>Trifolium repens</i>
15 <i>Centaurea stoebe</i>	32 <i>Melilotus albus</i>	49 <i>Verbascum thapsus</i>
16 <i>Cirsium vulgare</i>	33 <i>Phytolacca americana*</i>	50 <i>Vicia sativa*</i>
17 <i>Conyza canadensis*</i>	34 <i>Plantago lanceolata</i>	

326

327 Fig. 2



328

329

