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## **Dimensions of invasiveness: Links between local abundance, geographic range size, and habitat breadth in Europe's alien and native floras**

Trevor Fristoe, Milan Chytrý, Wayne Dawson, Franz Essl, Ruben Heleno, Holger Kreft, Noëlie Maurel, Jan Pergl, Petr Pyšek, Hanno Seebens, et al.

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2 **Main Manuscript for**

3 Dimensions of invasiveness: links between local abundance,  
4 geographic range size and habitat breadth in Europe's alien and  
5 native floras.

6

7 Trevor S Fristoe<sup>1\*</sup>, Milan Chytrý<sup>2</sup>, Wayne Dawson<sup>3</sup>, Franz Essl<sup>4</sup>, Ruben Heleno<sup>5</sup>, Holger Kreft<sup>6,7</sup>,  
8 Noëlie Maurel<sup>1</sup>, Jan Pergl<sup>8</sup>, Petr Pyšek<sup>8,9</sup>, Hanno Seebens<sup>10</sup>, Patrick Weigelt<sup>6</sup>, Pablo Vargas<sup>11</sup>,  
9 Qiang Yang<sup>1</sup>, Fabio Attorre<sup>12</sup>, Erwin Bergmeier<sup>13</sup>, Markus Bernhardt-Römermann<sup>14</sup>, Idoia  
10 Biurrun<sup>15</sup>, Steffen Boch<sup>16</sup>, Gianmaria Bonari<sup>17</sup>, Zoltán Botta-Dukát<sup>18</sup>, Hans Henrik Bruun<sup>19</sup>,  
11 Chaeho Byun<sup>20</sup>, Andraž Čarni<sup>21,22</sup>, Maria Laura Carranza<sup>23</sup>, Jane A Catford<sup>24</sup>, Bruno E. L.  
12 Cerabolini<sup>25</sup>, Eduardo Chacón-Madrugal<sup>26</sup>, Daniela Ciccarelli<sup>27</sup>, Renata Čušterevska<sup>28</sup>, Iris de  
13 Ronde<sup>29</sup>, Jürgen Dengler<sup>30,31,32</sup>, Valentin Golub<sup>33</sup>, Rense Haveman<sup>29</sup>, Nate Hough-Snee<sup>34</sup>, Ute  
14 Jandt<sup>32,35</sup>, Florian Jansen<sup>36</sup>, Anna Kuzemko<sup>37</sup>, Filip Kůzmič<sup>38</sup>, Jonathan Lenoir<sup>39</sup>, Armin  
15 Macanović<sup>40</sup>, Corrado Marcenò<sup>2</sup>, Adam Martin<sup>41</sup>, Sean T Michaletz<sup>42</sup>, Akira S Mori<sup>43</sup>, Ülo  
16 Niinemets<sup>44</sup>, Tomáš Peterka<sup>2</sup>, Remigiusz Pielech<sup>45,46</sup>, Valerijus Rašomavičius<sup>47</sup>, Solvita Rūsiņa<sup>48</sup>,  
17 Arildo S Dias<sup>49</sup>, Mária Šibíková<sup>50</sup>, Urban Šilc<sup>51</sup>, Angela Stanisci<sup>52</sup>, Steven Jansen<sup>53</sup>, Jens-  
18 Christian Svenning<sup>54</sup>, Grzegorz Swacha<sup>55</sup>, Fons van der Plas<sup>56</sup>, Kiril Vassilev<sup>57</sup>, and Mark van  
19 Kleunen<sup>1,58</sup>

20 <sup>1</sup>*Ecology, Department of Biology, University of Konstanz, Universitätsstrasse 10, D-78457*  
21 *Konstanz, Germany*

22 <sup>2</sup>*Department of Botany and Zoology, Faculty of Science, Masaryk University, Kottlářská 2, 611 37,*  
23 *Brno, Czech Republic*

24 <sup>3</sup>*Department of Biosciences, Durham University, South Road, Durham DH1 3LE, United Kingdom*

25 <sup>4</sup>*Bioinvasions, Global Change, Macroecology-research group, Division of Conservation Biology,*  
26 *Vegetation- and Landscape Ecology, Department of Botany and Biodiversity Research, University*  
27 *of Vienna, Rennweg 14, Vienna 1030, Austria*

28 <sup>5</sup>*Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, Coimbra,*  
29 *Portugal*

- 30 <sup>6</sup>*Biodiversity, Macroecology & Biogeography, University of Goettingen, Büsungenweg 1, D-37077*  
31 *Göttingen, Germany*
- 32 <sup>7</sup>*Centre of Biodiversity and Sustainable Land Use (CBL), University of Goettingen, Büsungenweg 1,*  
33 *D-37077 Göttingen, Germany*
- 34 <sup>8</sup>*Czech Academy of Sciences, Institute of Botany, Department of Invasion Ecology, CZ-252 43*  
35 *Průhonice, Czech Republic*
- 36 <sup>9</sup>*Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-128 44 Prague,*  
37 *Czech Republic*
- 38 <sup>10</sup> *Senckenberg Biodiversity and Climate Research Centre, Frankfurt am Main, Germany*
- 39 <sup>11</sup> *Real Jardín Botánico (RJB-CSIC), 28014-Madrid, Spain*
- 40 <sup>12</sup>*Environmental Biology, Sapienza University of Rome, P.le A. Moro 5, 00185 Roma, Italy*
- 41 <sup>13</sup> *Vegetation Analysis & Phytodiversity, University of Göttingen, Untere Karspüle 2, 37073*  
42 *Göttingen, Germany*
- 43 <sup>14</sup> *Institute of Ecology and Evolution, Friedrich Schiller University Jena, Dornburger Str. 159, DE-*  
44 *07743 Jena, Germany*
- 45 <sup>15</sup> *Plant Biology and Ecology, University of the Basque Country UPV/EHU, Apdo. 644, 48080*  
46 *Bilbao, Spain*
- 47 <sup>16</sup> *Biodiversity and Conservation Biology, WSL Swiss Federal Research Institute, Zürcherstrasse*  
48 *111, Switzerland*
- 49 <sup>17</sup> *Faculty of Science and Technology, Free University of Bolzano-Bozen, Piazza Università, 1,*  
50 *39100, Italy*
- 51 <sup>18</sup> *Centre for Ecological Research, Alkotmány u. 2-4, 2163 Vácrátót, Hungary*
- 52 <sup>19</sup> *Department of Biology, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen*
- 53 <sup>20</sup> *Department of Biological Sciences and Biotechnology, Andong National University, 1375*  
54 *Gyeongdong-ro, Andong, Gyeongsangbukdo, 36729, Korea*
- 55 <sup>21</sup> *Institute of Biology, Research Centre of the Slovenian Academy of Sciences and Arts, Novi trg*  
56 *2, 1000 Ljubljana, SI*
- 57 <sup>22</sup> *Faculty for Viticulture and Enology, University of Nova Gorica, Vipavska 13, 5000 Nova Gorica,*  
58 *SI*
- 59 <sup>23</sup> *Bioscience and Territory, EnivixLab, Univeristy of Molise, Contrada Fonte Lappone snc, 86090*  
60 *Pesche (IS), Italy*
- 61 <sup>24</sup> *Department of Geography, King's College London, 30 Aldwych, London, WC2B 2BG, UK*
- 62 <sup>25</sup> *Department of Biotechnologies and Life Sciences (DBSV), University of Insubria, via J.H.*  
63 *Dunant, 3 - I-21100 Varese – Italy*
- 64 <sup>26</sup> *Escuela de Biología, Universidad de Costa Rica, 11501-2060, Escuela de Biología, San José,*  
65 *Costa Rica*

- 66 <sup>27</sup> *Department of Biology, University of Pisa Via, Luca Ghini 13, 56126 Pisa, Italy*
- 67 <sup>28</sup> *Institute of Biology, Faculty of Natural Sciences and Mathematics, Ss. Cyril and Methodius*  
68 *University, Arhimedova 3, Skopje, North Macedonia*
- 69 <sup>29</sup> *Central Government Real Estate Agency, Ministry of the Interior and Kingdom Relations, PO*  
70 *Box 47, 6700AA Wageningen, The Netherlands*
- 71 <sup>30</sup> *Vegetation Ecology, Institute of Natural Resource Sciences (IUNR), Zurich University of Applied*  
72 *Sciences, Grüentalstr. 14, 8820 Wädenswil, Switzerland*
- 73 <sup>31</sup> *Plant Ecology, Bayreuth Center for Ecology and Environmental Research (BayCEER),*  
74 *University of Bayreuth, Universitätsstr. 30, 95447 Bayreuth, Germany*
- 75 <sup>32</sup> *German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig Deutscher Platz*  
76 *5E, 04103 Leipzig, Germany*
- 77 <sup>33</sup> *Laboratory of Phytocenology, Samara Federal Research Scientific Center RAS. Institute of*  
78 *Ecology of Volga River Basin RAS, Komzina 10, 445003.Togliatti, Russia*
- 79 <sup>34</sup> *Four Peaks Environmental Science and Data Solutions, Wenatchee, WA, USA 98801*
- 80 <sup>35</sup> *Institute of Biology/Geobotany and Botanical Garden, Martin-Luther-University Halle-*  
81 *Wittenberg, Am Kirchtor 1, DE 06108 Halle (Saale), Germany*
- 82 <sup>36</sup> *Faculty of Agricultural and Environmental Sciences, University of Rostock, Justus-von-Liebig-*  
83 *Weg 6, 18059 Rostock, Germany*
- 84 <sup>37</sup> *M.G. Kjolodny Institute of Botany, National Academy of Sciences of Ukraine,*  
85 *Tereschchenkivska, 2, 01601, Kyiv, Ukraine*
- 86 <sup>38</sup> *Jovan Hadži Institute of Biology, Research Centre of the Slovenian Academy of Sciences and*  
87 *Arts, Novi trg 2, 1000 Ljubljana, SI*
- 88 <sup>39</sup> *UR Ecologie et Dynamique des Systèmes Anthropisés (EDYSAN), UMR 7058 CNRS,*  
89 *Université de Picardie Jules Verne, 1 Rue des Louvels, 80037 Amiens Cedex 1, France*
- 90 <sup>40</sup> *Department of Biology, Faculty of Science, Center for Ecology and Natural Resources -*  
91 *Academician Sulejman Redžić, University of Sarajevo, Zmaja od Bosne 33-35, Sarajevo, Bosnia*  
92 *and Herzegovina*
- 93 <sup>41</sup> *Department of Physical and Environmental Sciences, University of Toronto Scarborough, 1265*  
94 *Military Trail, Toronto, Ontario, Canada*
- 95 <sup>42</sup> *Department of Botany and Biodiversity Research Centre, The University of British Columbia,*  
96 *6270 University Blvd., Room 3156, Vancouver, BC V6T 1Z4, Canada*
- 97 <sup>43</sup> *Graduate School of Environment and Information Sciences, Yokohama National University, 79-*  
98 *7 Tokiwadai, Hodogaya, Yokohama, Kanagawa 240-8501, Japan*
- 99 <sup>44</sup> *Chair of Crop Science and Plant Biology, Estonian University of Life Sciences, Kreutzwaldi 1,*  
100 *51006 Tartu, Estonia*
- 101 <sup>45</sup> *Department of Forest Biodiversity, University of Agriculture in Kraków, 29 Listopada 46, 31-*  
102 *425 Kraków, Poland*
- 103 <sup>46</sup> *Foundation for Biodiversity Research, Terenowa 4c/6, Wrocław, Poland*

- 104 <sup>47</sup> *Institute of Botany, Nature Research Centre, Žaliuju Ežeru Str. 49, 12200 Vilnius, Lithuania*
- 105 <sup>48</sup> *Department of Geography, Faculty of Geography and Earth Sciences, University of Latvia,*  
106 *Jelgavas iela 1, Riga, LV-1004, Latvia*
- 107 <sup>49</sup> *Department of Physical Geography, Goethe University, Altenhöferallee 1, 60438 Frankfurt am*  
108 *Main*
- 109 <sup>50</sup> *Department of Geobotany, Plant Science and Biodiversity Center, Slovak Academy of*  
110 *Sciences, Dúbravská cesta 9, 845 23 Bratislava*
- 111 <sup>51</sup> *Institute of Biology Research, Centre of the Slovenian Academy of Sciences and Arts, Novi trg*  
112 *2, 1000 Ljubljana, SI*
- 113 <sup>52</sup> *Department of Bioscience and Territory, EnvixLab, University of Molise, Via Duca degli Abruzzi*  
114 *s/n, 86039, Termoli, Italy*
- 115 <sup>53</sup> *Institute of Systematic Botany and Ecology, Ulm University, Albrecht-Einstein-Allee 11, 89081*  
116 *Ulm, Germany*
- 117 <sup>54</sup> *Center for Biodiversity Dynamics in a Changing World, Department of Biology, Aarhus*  
118 *University, Ny Munkegade 114, DK-8000 Aarhus C, Denmark*
- 119 <sup>55</sup> *Department of Vegetation Ecology, Botanical Garden, University of Wrocław,*  
120 *Przybyszewskiego 63, Wrocław, Poland*
- 121 <sup>56</sup> *Plant Ecology and Nature Conservation Group, Wageningen University, PO Box 47, 6700AA*  
122 *Wageningen, The Netherlands*
- 123 <sup>57</sup> *Department of Plant and Fungal Diversity and Resources, Institute of Biodiversity and*  
124 *Ecosystem Research, 23 Acad. G. Bonchev Str., 1113 Sofia, Bulgaria*
- 125 <sup>58</sup> *Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou*  
126 *University, Taizhou 318000, China*

127

128 \* Corresponding author: Trevor S Fristoe

129 **Email:** [trevor.fristoe@uni-konstanz.de](mailto:trevor.fristoe@uni-konstanz.de)

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141

142 **This PDF file includes:**

143 Main Text

144 Figures 1 to 4

145 Table 1

146

147 **Abstract**

148 Understanding drivers of success for alien species can inform on potential future invasions.  
149 Recent conceptual advances highlight that species may achieve invasiveness via performance  
150 along at least three distinct dimensions: (1) local abundance, (2) geographic range size, and (3)  
151 habitat breadth in naturalized distributions. Associations among these dimensions and the factors  
152 that determine success in each have yet to be assessed at large geographic scales. Here, we  
153 combine data from over 1 million vegetation plots covering the extent of Europe and its habitat  
154 diversity with databases on species' distributions, traits, and historical origins to provide a  
155 comprehensive assessment of invasiveness dimensions for the European alien seed-plant flora.  
156 Invasiveness dimensions are linked in alien distributions, leading to a continuum from overall poor  
157 invaders to super invaders –abundant, widespread aliens that invade diverse habitats. This  
158 pattern echoes relationships among analogous dimensions measured for native European  
159 species. Success along invasiveness dimensions was associated with details of alien species'  
160 introduction histories: earlier introduction dates were positively associated with all three  
161 dimensions, and consistent with theory based expectations, species originating from other  
162 continents, particularly acquisitive growth strategists, were among the most successful invaders  
163 in Europe. Despite general correlations among invasiveness dimensions, we identified habitats  
164 and traits associated with atypical patterns of success in only one or two dimensions – for  
165 example, the role of disturbed habitats in facilitating widespread specialists. We conclude that  
166 considering invasiveness within a multidimensional framework can provide insights into invasion  
167 processes, while also informing general understanding dynamics of species distributions.

168 **Significance Statement**

169 Invasive alien species pose major threats to biodiversity and ecosystems. However, identifying  
170 drivers of invasion success has been challenging, in part because species can achieve  
171 invasiveness in different ways, each corresponding to different aspects of demographics and  
172 distribution. Employing a multidimensional perspective of invasiveness to Europe's alien flora, we  
173 find species generally fall along an axis from overall poor invaders to super invaders that become  
174 abundant, widespread, and invade diverse habitats. Some species that deviate from this pattern  
175 are recently introduced and still spreading, but others represent atypical forms of invasiveness. In  
176 addition to identifying species traits and ecological circumstances associated with super invaders  
177 (e.g. intercontinental introductions), we explore drivers in atypical invasions, providing increased  
178 clarity into invasion processes.

179

180

181 **Main Text**

182

183 **Introduction**

184

185 Human socioeconomic activities are altering species' global distributions, bridging natural  
186 dispersal barriers through the accidental and intentional relocation of organisms, and opening  
187 opportunities for them to expand into new regions beyond their historic native ranges (1). The  
188 outcome of any given introduction event, however, is dependent on ecological and stochastic  
189 processes, and many introduced alien species fail to establish and persist (2, 3). But even

190 species that do achieve persistent, self-sustaining populations (i.e., become naturalized *sensu*  
191 (4)) show varying degrees of success (i.e., invasiveness) in newly occupied regions. This has  
192 been true for natural colonization events throughout Earth's history (e.g., on islands (5, 6) and  
193 during continental biotic interchanges (7–9)), and is certainly the case for the ongoing surge of  
194 human-mediated introductions (10–12). Disentangling the factors that lead to invasion success  
195 provides an opportunity not only for anticipating and mediating future anthropogenic invasions,  
196 but also for better understanding the dynamics underlying natural range expansions (13).

197  
198 Quantifying a species' success in invading the alien range is complex, a fact reflected in the  
199 diverse criteria applied by different authorities when deciding whether or not to classify  
200 naturalized species as invasive (14). Recent efforts have therefore recognized that invasiveness  
201 cannot be captured by a single metric, but rather encompasses multiple aspects of ecological  
202 success and impact (15, 16). Some proposed metrics, such as spread rate and socio-economic  
203 impacts, are difficult to quantify for large numbers of species (4, 17). However, Rabinowitz's  
204 three-dimensional scheme for characterizing the rarity or commonness of species in their native  
205 distributions (18, 19) has been successfully co-opted as a valuable perspective for better  
206 understanding the success of alien species (16, 20, 21). Applied in the context of introduced  
207 species, this framework recognizes the potential for established aliens to vary along at least three  
208 demographic dimensions of invasiveness: 1) in local abundance within the naturalized range, 2)  
209 in geographic range size or extent of the naturalized range, and 3) in habitat breadth in the  
210 naturalized range (16). We subsequently distinguish these metrics as dimensions of invasiveness  
211 when measured in the naturalized distributions of alien species, and dimensions of commonness  
212 when measured in species native distributions.

213  
214 Considering invasiveness within a multidimensional framework is particularly important if species  
215 vary independently among different dimensions (16, 21). Such a scenario opens the possibility for  
216 aliens to achieve invasion success in many different ways (Fig. 1). In other words, there could  
217 exist different forms of invasiveness, similar to the different forms of rarity or commonness  
218 originally proposed by Rabinowitz (19). On the other hand, theoretical concepts and empirical  
219 examples suggest correlations between Rabinowitz's dimensions of commonness among species  
220 in their native distributions (6, 22, 23). For example, a positive relationship between local  
221 abundance and extent of geographic occurrence or range size has been documented at various  
222 scales for numerous taxa (24–26), including plants (24, 27–31), with niche breadth proposed as a  
223 linking mechanism (24, 26, 32). If the processes that generate these patterns in native  
224 distributions act similarly in species alien distributions, some of the forms of invasiveness outlined  
225 in Fig. 1 should be less likely to occur than others. More specifically, if the invasiveness  
226 dimensions are correlated, species should vary from excelling (abundant, widespread,  
227 generalists; form AWG in Fig. 1) to performing poorly (scarce, restricted, specialists; form 0 in Fig.  
228 1) in all three invasiveness dimensions (33). On the other hand, these macroecological patterns  
229 are not without exception, and a recent assessment found little support for correlations among  
230 commonness dimensions in Europe's native flora (34). Alien distributions may further differ  
231 because aliens vary in their residence time and particularly recently introduced species may be in  
232 disequilibrium and still increasing along one or more of the invasiveness dimensions (21, 35–37).  
233 In line with these alternatives, a continuum from overall poor invaders to species succeeding in all  
234 three dimensions has been documented for the regional alien flora of French grassland  
235 communities (20), while associations among dimensions were found to be low for the herbaceous  
236 alien flora of Southeast Australia (16). The correspondence among different invasiveness  
237 dimensions at broader geographic scales has yet to be assessed.

238  
239 Functional traits play a role in mediating invasion processes, but efforts to identify characteristics  
240 of successful invaders have generally resulted in few or inconsistent associations (38, 39).  
241 However, distinguishing between different components of invasiveness may provide additional  
242 clarity if each is influenced by different traits, or if the same trait has contrasting effects on  
243 different dimensions (15, 16, 21, 40, 41). For example, many plant traits are associated with

244 general trade-offs between rapid growth (i.e., acquisitive growth strategies) versus stress  
245 tolerance and survival (i.e., conservative growth strategies) (42–44), and one can hypothesize  
246 scenarios where these divergent strategies are associated with success in different dimensions of  
247 invasiveness (40, 41). Another example are specialized adaptations for long-distance dispersal  
248 that may promote rapid range expansion, both in extent and into new habitats, but likely do not  
249 provide any advantages that would influence local abundances (45, 46). For habitat specialists,  
250 their specific habitat associations may additionally be important for determining whether or not  
251 they become widespread (31).

252  
253 A number of hypotheses for invasion success additionally emphasize the importance of unique  
254 ecological dynamics that emerge when species are decoupled from constraints experienced in  
255 their native environments (47). For example, because species are able to occupy unfilled niches  
256 where introduced (i.e. Darwin's naturalization hypothesis (48, 49)) or because they leave behind  
257 important herbivores, competitors, or pathogens that limit populations in the native distribution  
258 (i.e., enemy release (50, 51)). These mechanisms may be less likely when species expand into  
259 areas near the native range, for example during natural range expansions or intra-continental  
260 introductions, as the alien individuals are more likely to encounter conditions similar to those that  
261 limited their native distribution compared to species introduced from further abroad (e.g., those  
262 with extra-continental origins) (52–54).

263  
264 Here, we combine vegetation-plot data covering Europe (55) with databases of alien and native  
265 distributions (56, 57), plant traits (58, 59), and historical dates of introduction (60) to provide a  
266 comprehensive assessment of multidimensional invasion success for the European alien seed-  
267 plant flora. First, we test for correlations among local abundance, geographic extent, and habitat  
268 breadth of alien species in their naturalized distributions and classify species into one of the eight  
269 forms of invasiveness (Fig. 1). We ask whether some forms of invasiveness rarely occur, and  
270 specifically whether species tend to fit along a continuum ranging from generally poor invaders to  
271 super invaders – species excelling in all three dimensions. In addition, we compare relationships  
272 among dimensions of invasiveness to those among dimensions of commonness measured for  
273 Europe's native flora, assessing similarities and differences in patterns of distribution between  
274 contexts. Next, we explore likely drivers of each invasiveness dimension, testing whether the year  
275 of first alien occurrence in Europe, functional traits related to ecological strategies, specialized  
276 adaptations for long-distance dispersal, habitat associations, and region of origin explain different  
277 forms of invasion success.

278  
279

## 280 **Results**

281

### 282 *Associations among dimensions*

283 Bivariate correlation tests showed that all three dimensions of invasiveness were significantly  
284 positively correlated (Fig. 2e-i). The strongest link in the naturalized distributions of alien species  
285 was between the geographic extent and local abundance dimensions ( $r = 0.48$ ,  $p < 0.001$ );  
286 correlations between either of these two dimensions and the habitat breadth dimension were  
287 relatively low, but significant (abundance-habitat breadth:  $r = 0.24$ ,  $p < 0.001$ ; extent-habitat  
288 breadth:  $r = 0.23$ ,  $p < 0.001$ ). Patterns were very similar for dimensions of commonness in native  
289 European distributions (including from the native distributions of intra-continental aliens), though  
290 correlations involving habitat breadth were stronger in this context (abundance-extent:  $r = 0.41$ ,  $p$   
291  $< 0.001$ ; abundance-habitat breadth:  $r = 0.42$ ,  $p < 0.001$ ; extent-habitat breadth:  $r = 0.58$ ,  $p < 0.001$ ;  
292 Fig. 2a-c). Our results additionally suggest that correlations among dimensions increase as  
293 distributions are given time to approach equilibrium. When alien species were grouped by their year  
294 of first alien occurrence, correlations among invasiveness dimensions were strongest for the subset  
295 of species with dates prior to 1800 ( $n = 326$ ; abundance-extent:  $r = 0.51$ ,  $p < 0.001$ ; abundance-  
296 habitat breadth:  $r = 0.34$ ,  $p < 0.001$ ; extent-habitat breadth:  $r = 0.34$ ,  $p < 0.001$ ), intermediate for  
297 those with dates between 1800 and 1900 ( $n = 336$ ; abundance-extent:  $r = 0.47$ ,  $p < 0.001$ ;



298 abundance-habitat breadth:  $r = 0.20$ ,  $p < 0.001$ ; extent-habitat breadth:  $r = 0.24$ ,  $p < 0.001$ ), and  
299 weakest for species introduced from 1900 onwards, where correlations between habitat breadth  
300 and the other two dimensions were not significant ( $n = 174$ ; abundance-extent:  $r = 0.37$ ,  $p < 0.001$ ;  
301 abundance-habitat breadth:  $r = 0.10$ ,  $p = 0.18$ ; extent-habitat breadth:  $r = 0.13$ ,  $p = 0.09$ ). We also  
302 identified interactions in the relationships among dimensions: high abundance was more strongly  
303 associated with widespread extent for habitat generalist species than for habitat specialists in alien  
304 distributions (adjusted  $R^2$  for interaction model = 0.25; SI Appendix, Table S1; Fig. 2h) as well as  
305 in native distributions (adjusted  $R^2 = 0.38$ ; SI Appendix, Table S2; Fig. 2d). These patterns were  
306 consistent when analyzed with PGLS regression (SI Appendix, Table S3 and S4) and for the subset  
307 of extra-European aliens (i.e. those with native distributions completely outside of the continent; SI  
308 Appendix, Tables S5 and S6).

309  
310 The general correspondence among invasiveness dimensions is evident when visualizing all three  
311 simultaneously, with most species falling along an axis from low to high values in all three  
312 dimensions (Fig. 2i and j). Randomization tests further revealed how the filling of this three-  
313 dimensional invasiveness space differed from null expectations (i.e. a scenario where dimensions  
314 are not correlated; Fig. 3). Poor invaders (form 0) and super invaders (form AWG) were the only  
315 invasiveness categories that included more species than expected by chance. When analyzing the  
316 full species sample, the four forms of invasiveness characterized by high abundance and low extent  
317 or *vice versa* (form A, form W, form AG, and form WG; see Fig. 1) were significantly under-  
318 represented. Some details in the associations among invasiveness dimensions changed as the  
319 sample of species was increasingly restricted to exclude those with widespread native distributions  
320 in Europe (eventually including only extra-European aliens). For these restricted species subsets,  
321 widespread extent showed stronger links with habitat generalism than with high abundance (i.e.,  
322 form A and form WG were no longer significantly under-represented and form AW and form G  
323 rarely occurred). Otherwise, general patterns remained consistent across species subsets: poor  
324 and super invaders (form 0 and form AWG, respectively) were over-represented, scarce specialist  
325 species were rarely widespread (form W was under-represented), and abundant generalists with  
326 restricted range extents were rare (form AG was under-represented). Similarly, in native European  
327 distributions, forms 0 and AWG were the only over-represented forms of commonness, with over  
328 half of species categorized into one of the two (SI Appendix, Table. S7). All other forms of  
329 commonness were underrepresented. Results were largely consistent when the 0.25 and 0.75  
330 quantile of each trait, rather than the median, were used to classify species into invasiveness or  
331 commonness forms (SI Appendix, Fig. S1 and Table S7).

### 332 333 *Drivers of invasiveness dimensions*

334 We found that historical details of species introductions—geographic origins (i.e., extra- vs intra-  
335 European) and year of first record—were generally more important in explaining success along  
336 dimensions of invasiveness than plant traits. Regression analyses revealed that values of all three  
337 invasiveness dimensions tended to be higher for species with earlier recorded introductions in  
338 Europe (Table 1; Fig. 4). For habitat breadth, the slope of the relationship with the year of first  
339 record was steeper for extra-European aliens than for intra-European aliens (i.e. species introduced  
340 from native regions elsewhere in Europe; Fig. 4). Geographic origins and species traits additionally  
341 influenced invasiveness dimensions (Table 1; Fig. 4; abundance: adjusted  $R^2 = 0.19$ ; extent:  
342 adjusted  $R^2 = 0.27$ ; habitat breadth: adjusted  $R^2 = 0.04$ ). For the abundance and extent dimensions,  
343 geographic origins (i.e., extra- vs intra-European) and year of first record contributed the majority  
344 of explained variance (additional variance explained: origin for abundance = 0.09; first record for  
345 abundance = 0.05; origin for extent = 0.17; first record for extent = 0.09). Explanatory power of  
346 particular plant traits was therefore generally low for all three invasiveness dimensions.

347  
348 For abundance in the naturalized range, the influence of plant height, seed mass, and investment  
349 in stem and leaf structure (together captured by  $PC_{Size}$ ; SI Appendix, section 'Trait data', Table S8  
350 and Fig. S2) differed between intra- and extra-European aliens. Abundance increased with  
351 increasing values of  $PC_{Size}$  for intra-European aliens (simple slope:  $p < 0.02$ ) but showed little

352 relationship for extra-European aliens (simple slope:  $p = 0.65$ ). This resulted in the largest  
353 differences in abundance between the two groups occurring in short-statured plants with small  
354 seeds and low investment in stem and leaf structure (Fig. 4). Position along the leaf economics  
355 spectrum ( $PC_{Econ}$ ; SI Appendix, section 'Trait data', Table S8 and Fig. S2) (42, 43) also influenced  
356 naturalized abundance differently for intra- and extra-European aliens. While abundance showed  
357 a non-significant decrease with increasingly acquisitive growth strategies (i.e. higher  $PC_{Econ}$  values  
358 reflecting higher leaf N content, leaf area, and specific leaf area) in intra-European aliens (simple  
359 slope:  $p = 0.23$ ), an increase in abundances was seen with increasing  $PC_{Econ}$  values in extra-  
360 European aliens (simple slope:  $p = 0.03$ ). Overall, this gave rise to a pattern whereby abundances  
361 were highest for acquisitive species originating from outside Europe but lowest for acquisitive  
362 species introduced from within Europe (Fig. 4). Graminoids tended to occur at higher abundances  
363 and species with epizoochorous or endozoochorous long-distance dispersal syndromes tended to  
364 occur at lower abundances than species without such specializations (Table 1). Traits showed  
365 generally weak relationships with abundance in native European distributions (adjusted  $R^2 = 0.11$ ;  
366 SI appendix Tables S9-11); growth form was the strongest explanatory variable (additional variance  
367 explained = 0.10), being lower in forbs than in other groups.

368  
369 Geographic extent of naturalized distributions was generally higher for extra-European aliens and  
370 decreased further in small-sized intra-European aliens (i.e., low  $PC_{Size}$  values; simple slope extra-  
371 European:  $p = 0.14$ ; simple slope intra-European:  $p < 0.01$ ; Table 1; Fig. 4). Naturalized extent was  
372 also higher for species with acquisitive growth strategies (high  $PC_{Econ}$ ), regardless of their  
373 geographic origin. Contrary to predictions, the capacity for long-distance dispersal, specifically  
374 anemochory, had a general negative effect on naturalized extent (Table 1). For geographic extent  
375 in native distributions (adjusted  $R^2 = 0.10$ ; SI appendix Tables S9-11), growth form was the  
376 strongest explanatory variable (additional variance explained = 0.05), being greatest for graminoids  
377 and smallest for shrubs. Though we additionally detected weak, but significant, negative effects of  
378  $PC_{Size}$ , and positive effects for  $PC_{Econ}$  and seed dispersal through endozoochory.

379  
380 Habitat breadth in naturalized distributions was generally higher for graminoids and for trees, but  
381 after accounting for this effect, decreased with  $PC_{Size}$  in extra-European aliens (simple slope extra-  
382 European:  $p = 0.02$ ; simple slope intra-European:  $p = 0.80$ ; Table 1; Fig. 4). As was the case in  
383 naturalized distributions, traits were generally poor predictors of habitat breadth in native  
384 distributions (adjusted  $R^2 = 0.03$ ; SI appendix Tables S9-11). Patterns for all three invasiveness  
385 dimensions were generally similar when data was analyzed with PGLS regression, though some  
386 trait effects were no longer significant ( $PC_{Size}$ -origin interaction on naturalized abundance:  $p = 0.06$ ;  
387  $PC_{Econ}$ -origin interaction for naturalized abundance:  $p = 0.12$ ;  $PC_{Econ}$  for naturalized extent:  $p =$   
388  $0.07$ ;  $PC_{Size}$ -origin interaction for naturalized habitat breadth:  $p = 0.06$ ; SI Appendix, Table S12).

### 389 *Characteristics of different forms of invasiveness*

390  
391 In addition to identifying conditions associated with each individual dimension of invasiveness, we  
392 found general patterns in the characteristics of alien species within each of the eight forms of  
393 invasiveness (SI appendix, Fig. S3 and Tables S13-S17 for full results of randomization tests). Poor  
394 invaders (form 0) and restricted range generalists (form G and form AG) overwhelmingly comprised  
395 intra-European aliens. In contrast, super-invaders (form AWG) and abundant, widespread  
396 specialists (form AW) were disproportionately composed of extra-European aliens (SI appendix,  
397 Fig. S3 and Table S13). Species that excelled only in the abundance dimension (form A) tended  
398 towards conservative growth strategies (low  $PC_{Econ}$ ), regardless of origin. Otherwise, for intra-  
399 European aliens, habitat generalist species that were also abundant (form AG and form AWG)  
400 tended to be larger in size (high  $PC_{Size}$ ); poor invaders (form 0) and species that excelled in only  
401 the habitat breadth or abundance dimensions (form G and form A) were smaller (low  $PC_{Size}$ ), and  
402 widespread generalists tended towards acquisitive growth strategies (high  $PC_{Econ}$ ; SI Appendix,

403 Table S14). Differences in growth forms among forms of invasiveness were largely consistent with  
404 the results for PC<sub>Size</sub> and PC<sub>Econ</sub> (SI Appendix, Table S15).

405

406 All eight forms of invasiveness included species with dates of first alien occurrence ranging from at  
407 least the mid sixteenth century to the turn of the twenty-first century (SI appendix, Fig. S3).  
408 However, super invaders (form AWG) and intra-European aliens classified in form WG were  
409 associated with earlier recorded dates of introduction in Europe (SI appendix, Fig. S3 and Table  
410 S16). In contrast, poor invaders (form 0), species that succeeded in only the habitat breadth or the  
411 abundance dimensions (form G and form A) were associated with relatively recent dates of  
412 introductions. Species specialized for long-distance dispersal did not show any strong patterns  
413 besides the over-representation of specialized dispersers among extra-European aliens classified  
414 as overall poor invaders (form 0) and their under-representation among form AW species (SI  
415 Appendix, Table S17).

416

#### 417 *Habitats of specialists*

418 We found that, on average, the habitats occupied by species that were habitat specialists in their  
419 naturalized distributions (invasiveness form 0, form A, form W, and form AW) differed in area of  
420 coverage across Europe ( $F = 2.71$ ,  $p = 0.04$ ; SI Appendix, Fig. S4a and b). Specifically, alien  
421 species in form AW occurred in the most widespread habitats, though differences were small,  
422 variation was high, and this group was only statistically distinguishable from poor invaders (form 0;  
423 Tukey HSD test:  $p = 0.05$ ). Form AW alien species also showed a strong association with ruderal  
424 habitats; this was the only habitat where either invasiveness form of widespread habitat specialists  
425 (form W or AW) were overrepresented (SI Appendix, Fig. S4c). In native distributions, widespread  
426 habitat specialists also occurred in more widespread habitats ( $F = 10.89$ ,  $p < 0.001$ ; SI Appendix,  
427 Fig. S5a and b). Abundant habitat specialists with restricted ranges (form A) in particular occurred  
428 in habitats with limited area in Europe. Notably, habitat specialists that were widespread in their  
429 native European distributions (form W and form AW) were overrepresented in cropland habitats,  
430 the most widespread habitat in Europe, while those that also reached high abundances (form AW)  
431 were additionally overrepresented in ruderal habitats (SI Appendix, Fig. S5c).

432

433

## 434 **Discussion**

435

436 Our analysis of multidimensional invasion success in Europe's alien flora demonstrates that local  
437 abundance, range extent, and habitat breadth of naturalized distributions are positively  
438 associated at the continental scale. Most species fall along a spectrum from overall poor invaders  
439 to super invaders that excel in all three dimensions. These results echo patterns that we found for  
440 dimensions of commonness measured from the distributions of native European flora, and that  
441 have been previously documented in the native distributions of various taxa (23–26, 33). This  
442 suggests that similar mechanisms structure alien and native distributions at macroecological  
443 scales. Our finding of positive associations between abundance and geographic extent in the  
444 distributions of both native and alien species may seem at odds with a recent study that found low  
445 support for similar correlations in native European flora (34). However, this apparent discrepancy  
446 can be explained by our use of maximum abundance as a proxy of potential for local dominance  
447 (16, 61, 62), rather than averaging abundances across the entire range. This is consistent with  
448 previous studies that have found stronger abundance-extent relationships when using measures  
449 of maximum abundance (63). For alien distributions, our results largely correspond with those  
450 from a regional assessment of French grassland communities (20), but contrast with findings from  
451 Southeast Australia (16), perhaps reflecting that species introductions in Oceania have primarily  
452 occurred more recently and aliens there may not have had the necessary time to expand along  
453 each dimension (60). Indeed, our results suggest that many alien distributions have not reached  
454 equilibrium (37). Correlations among invasiveness dimensions were strongest for plant species  
455 with earlier dates of introduction, indicating that deviations from general patterns are at least  
456 partially driven by time lags in invasion processes (35, 36). In addition to earlier dates of

457 introduction, extra-continental origins were associated with higher performance along all three  
458 dimensions of invasiveness. Species functional traits, on the other hand, were typically poor  
459 predictors of dimensions in both alien and native distributions. This is perhaps unsurprising  
460 considering the diversity of successful ecological and life-history strategies that can be observed  
461 within and across natural systems (64). Nevertheless, we did find a number of significant trait  
462 effects, often showing interactions within the context of alien species' geographic origins, that are  
463 in line with hypothesized mechanisms of invasion (see text below). Taken together, our analyses  
464 identified characteristics of species and their introduction histories that help to explain why they  
465 showed success in only one, two, or in all three dimensions.

466  
467 The strongest correlation among invasiveness dimensions was between local abundance and  
468 geographic extent and there are many reasons to expect that these features of distributions  
469 should be linked. For example, the ability to maintain high population density reduces the  
470 probability of stochastic local extirpation and could facilitate the persistence of populations in  
471 more areas (65). Both local abundance and area of occupancy also influence the production of  
472 propagules and therefore the potential to colonize new regions and habitats or to bolster  
473 populations in previously colonized areas (66, 67). In addition, high local abundance should  
474 similarly increase the likelihood of further human-assisted dispersal (68, 69). Efforts to  
475 understand the widespread occurrence of so-called positive abundance-distribution relationships  
476 among species native distributions have so far led only to a general consensus that several  
477 interacting, rather than one single, mechanisms are likely at play (26, 70). Considering that even  
478 the direction of causality in these relationship remains unclear, it could be expected that species  
479 excelling in either of these invasiveness dimensions may eventually increase in the other if  
480 provided the opportunity and time – especially given the higher strength of correlation between  
481 these dimensions for species with longer residence times (i.e., earlier recorded dates of first  
482 occurrence).

483  
484 Our results, however, suggest that investment in rapid growth may be one path for aliens to  
485 become widespread without necessarily reaching high abundances locally. Acquisitive traits have  
486 been associated with range filling in native distributions (46), and we found that high values of  
487 trait  $PC_{Econ}$ , indicating acquisitive growth strategies, were associated with larger extents for native  
488 and naturalized ranges. But we found that intra-continental aliens with these traits showed lower  
489 naturalized abundance and were over-represented among the relatively few generalist species  
490 that were locally scarce but widespread in their naturalized distributions (see SI appendix, Fig.  
491 S3). In contrast, locally abundant species with restricted naturalized ranges tended to show  
492 conservative growth strategies. However, we found that many of the forms of invasiveness  
493 characterized by restricted geographic extent were associated with more recent introductions,  
494 suggesting that these patterns are influenced by time lags in invasion processes and that some of  
495 these species are likely to continue to expand their ranges in the future (35). This is potentially  
496 true even for species that currently appear to be overall poor invaders, and note should be taken  
497 if they begin to increase in any of the three dimensions.

498  
499 We predicted that alien species with diaspores adapted to long-distance dispersal should have  
500 broader naturalized extents. A rather modest increase in extent for endozoochorous species  
501 indicates that this may be the case for native distributions, but we found the opposite pattern for  
502 alien distributions, particularly for anemochorous aliens. Some potential reasons are that alien  
503 plants might be mostly dispersed by anthropogenic vectors, via many short-distance stepwise  
504 dispersal events (e.g., clonal spread, myrmecochory, barochory), or through stochastic events or  
505 other vectors for which long-distance dispersal syndromes have a negligible, or even negative  
506 effect (71, 72). For epizoochorous and endozoochorous aliens, specialized diaspores were also  
507 associated with lower naturalized abundances, suggesting that these adaptations may aid in the  
508 rapid colonization of newly available sites, but decrease establishment success (e.g., fugitive  
509 species concept; (73)). Plant height, on the other hand, is also associated with dispersal ability

510 and establishment success and was positively associated with naturalized extent in intra-  
511 European aliens (74, 75).

512  
513 Habitat breadth was less strongly correlated with the other two invasiveness dimensions, but our  
514 results reveal its important links in the invasion process. Locally abundant alien species were  
515 more likely to be widespread when they were also habitat generalists in their naturalized range  
516 (see figure 2h, see also (76)). This link was particularly evident in analyses restricted to aliens  
517 originating from outside of Europe (see Fig. 3), which already tended to be among the most  
518 abundant invaders in the region (see Fig. 4). Species capable of persisting in a wider variety of  
519 environments should generally have larger potential distributions (23, 77), but for habitat  
520 specialists, we found that their specific habitat associations influenced whether or not alien  
521 species were widespread: habitats that are common across Europe (though this effect was  
522 relatively weak and potentially sensitive to our coarse measures of habitat coverage), ruderal  
523 habitats in particular, were associated with larger naturalized range sizes (SI Appendix, Fig. S3).  
524 The role of disturbed environments in facilitating invasions may help to explain why links between  
525 habitat breadth and the other two dimensions were weaker in alien compared to native  
526 distributions (78). However, high abundance and widespread distributions were also associated  
527 with ruderal habitats, and additionally croplands, for native habitat specialists. The ability to  
528 capitalize on these widespread and expanding human modified environments appears to provide  
529 opportunities for some native as well as alien plants. Perhaps unsurprisingly, the functional traits  
530 included in our study were generally poor predictors of habitat breadth in native and alien  
531 distributions. Measures such as the breadth of environmental tolerances or the degree of  
532 phenotypic plasticity are currently not available for large numbers of species, but would potentially  
533 be informative (79). Habitat breadth in the native distribution could also prove fruitful in predicting  
534 success in this invasiveness dimension for cases where data is available (69, 80, 81), as has  
535 been shown for abundance (82).

536  
537 One of the most striking patterns in our analyses was the prominence of aliens originating from  
538 other continents among the most invasive species in Europe. These species typically reached  
539 higher local abundances and became naturalized over a wider geographic extent than aliens  
540 originating within the continent. The steeper relationship between date of first occurrence with  
541 habitat breadth indicates that extra-European aliens also spread more rapidly among habitats in  
542 their non-native distributions (see Fig. 4). These results are in line with previous suggestions that  
543 species expanding their range in response to climate change, either through natural dispersal or  
544 human assisted migration, pose relatively low risk of becoming invasive in their new  
545 environments (54). However, we note that while intracontinental aliens were underrepresented  
546 among the worst invaders of Europe, they were not completely absent from these groups and  
547 more research is needed to fully understand the factors that determine their success (83).

548  
549 We found that the difference in abundance between intra- and extra-European aliens was  
550 dependent on traits that mark a general trade-off between rapid growth and increased survival,  
551 consistent with expectations of the enemy release hypothesis (51). Acquisitive growth strategists  
552 are particularly vulnerable to pathogens, herbivores, and competitors (84–86), suggesting a  
553 higher potential to benefit from enemy release (87, 88), but escape from biotic constraints is less  
554 likely when species are introduced to areas near their native distributions. Indeed, while  
555 acquisitive species introduced from outside of Europe were generally the most abundant and  
556 widespread aliens, we found that those originating from within the continent were typically scarce  
557 where naturalized. Larger species that invest in stem and leaf structure (high  $PC_{Size}$ ) and  
558 conservative growth strategies (low  $PC_{Econ}$ ) – traits associated with increased resistance to biotic  
559 enemies (84–86, 89) – tended to reach intermediate abundances whether they originated from  
560 inside or outside Europe. Unburdened from biotic constraints and capable of rapid growth,  
561 acquisitive extra-European aliens may be particularly suited for outcompeting native species and  
562 other aliens in disturbed habitats where the availabilities of resources such as light or nitrogen

563 tend to be higher. As human activities continue to alter natural landscapes, we should therefore  
564 expect these species to find increasing success as invaders into the future (90, 91).

565

#### 566 *Insights from a multidimensional perspective of invasiveness*

567 While distinguishing among different components of species naturalized distributions has been  
568 suggested as an important step in understanding the drivers of biological invasion (16, 20, 21),  
569 our assessment of the European alien flora, as well as the native flora, shows how different  
570 measures of invasion success or commonness are largely entangled; species capable of  
571 reaching high local abundances are also generally capable of occupying large areas and many  
572 different habitats. Indeed, deviations from this general pattern were greater for alien species with  
573 more recent introductions (e.g., post 1900), emphasizing that these species have not yet reached  
574 their full potential along some of the invasiveness dimensions. However, beyond clarifying some  
575 of the species characteristics and ecological processes that facilitate super invaders (e.g., extra-  
576 European origins), our analyses have also identified certain cases where the same trait can have  
577 divergent influence on invasiveness in different dimensions (e.g., position along the leaf  
578 economics spectrum has opposite effects on naturalized abundance and extent for intra-  
579 European aliens). In addition, by exploring exceptions to the general relationships, we identify  
580 traits and habitats that are associated with atypical invasion patterns. In short, despite the links  
581 between abundance, geographic extent, and habitat breadth, the dimensions of invasiveness  
582 framework has proven to be a valuable tool for making sense of current patterns of naturalization,  
583 anticipating future invasions, and generally improving our understanding of the dynamics of  
584 species distributions.

585

586

#### 587 **Materials and Methods**

588

589 Flow diagrams illustrating the databases and analyses used in this study are provided in SI  
590 Appendix, Fig. S6 and S7. Data and R code used for analyses can be found in supplemental data  
591 files S1-6.

592

#### 593 *Quantifying extent*

594 The geographic extent of naturalization for Europe's alien flora was measured using the Global  
595 Naturalized Alien Flora (GloNAF) database (56, 92, 93) (downloaded July 24, 2019). It consists of  
596 lists of alien plants (species and infraspecific taxa) documented for 861 regions covering the  
597 globe, with regions ranging from countries to smaller geopolitical units such as states, provinces,  
598 or individual islands (see SI Appendix, Fig. S8 for the distribution of geographic areas of  
599 European regions included in this study). For the purpose of this study, we included only seed-  
600 plants, gathered data at the species level by merging subspecies or varieties, and, when detailed  
601 information was available, we restricted alien occurrences to only those where a species was  
602 confirmed as naturalized in a region. We extracted data from GloNAF for the 5,653 species that  
603 have become naturalized in at least one region of Europe, with boundaries as defined by Ref.  
604 (94). Because abundance and habitat-breadth data covered only Europe (see below), our  
605 measure of geographic extent for each species was taken as the number of regions where they  
606 are reported as naturalized within the continent. Many of Europe's alien species are introduced  
607 from regions of native distributions elsewhere within the continent (intra-European aliens),  
608 meaning that the upper possible number of naturalized regions varied among species. Using  
609 native range data from Euro+Med PlantBase (57), we performed additional assessments to  
610 confirm that this constraint did not have a substantial influence on our measure of naturalized  
611 geographic range size (see SI Appendix, section 'Comparing extent measures'). We used the  
612 number of regions in the Euro+Med PlantBase where species were reported as native as our  
613 measure of extent for native distributions (available for 19,472 European species).

614

#### 615 *Quantifying abundance*

616 For metrics of local abundance in species' naturalized or native range, we used data on their  
617 relative cover measured in vegetation-plots compiled by the European Vegetation Archive (EVA)  
618 (55), a repository of data from over 1 million plots from vegetation surveys spanning all of Europe  
619 (downloaded on March 3, 2019). As a proxy for species capacity to become dominant, we used  
620 the maximum of spatially aggregated cover values as our measure of abundance for the species  
621 with sufficient data ( $n = 945$  for alien distributions;  $n = 6,052$  for native distributions; see SI  
622 Appendix, sections 'Quantifying abundance' and 'Matching between GloNAF and EVA' for details  
623 and Databases S1 and S2 for species lists).

624

#### 625 *Quantifying habitat breadth*

626 Each EVA survey plot was assigned to one of 229 habitat types of the European Nature  
627 Information System (EUNIS) using the classification expert system EUNIS-ESy ver. 2020-06-08  
628 (95). These habitat types were further merged into 47 broader habitat types used in this study (SI  
629 Appendix, Table S18). Habitat classification was possible for 66% of the nearly 390,000 EVA  
630 plots that included aliens, and 60% of over 1.2 million plots that included native species; these  
631 were used to quantify the habitat breadth of species naturalized and native ranges respectively.  
632 Because not all habitat types are equally distinct (e.g., wet and mesic grasslands are more similar  
633 to each other than either is to taiga), our measure of habitat breadth accounts for floral similarity  
634 among habitats by calculating the effective habitat number for each species following the method  
635 in Ref. (96) (see SI Appendix, section 'Effective habitat number' and Fig. S9). In addition to  
636 calculating habitat breadth, we determined the habitat where each species most frequently  
637 occurred by aggregating EVA plots in  $1^\circ \times 1^\circ$  grid cells and counting the number of grid cells  
638 where each species was observed in each habitat.

639

#### 640 *Assessing associations among dimensions*

641 We used a number of complementary approaches to test for associations among the three  
642 dimensions of invasiveness or commonness. In all cases, dimension measures were log-  
643 transformed prior to analysis. First, we performed pairwise correlation tests between dimensions  
644 using the Pearson correlation coefficient. To assess the influence of residence time on the  
645 association among invasiveness dimensions, we additionally performed correlation tests on three  
646 subsets of alien species depending on their first recorded year of alien occurrence in Europe:  
647 those with first records before 1800, those with first records from 1800 to 1900, and those with  
648 the first record year from 1900 onwards. Information on species' first record as an introduced  
649 alien in Europe came from Ref. (60). Second, in order to test for more complex relationships  
650 among dimensions, we performed linear regression with geographic extent as the response, with  
651 an interaction between abundance and habitat breadth as explanatory variables. This analysis  
652 was performed for the full native species dataset, full alien species dataset, and also for a  
653 restricted subset including only the alien species originating from entirely outside of Europe  
654 (extra-European aliens). In order to ensure that results were robust to phylogenetic non-  
655 independence in our species samples, we additionally tested the same relationships using  
656 phylogenetic generalized least squares (PGLS) regression using the 'ape' and 'nlme' packages in  
657 R (97, 98). Phylogenetic analyses were based on a global seed-plant phylogeny from Ref. (99)  
658 with 26 missing species added to the root of their respective genera or family following the  
659 methods in Ref. (3).

660

661 The third approach was to classify species into the eight different forms of invasiveness (Fig. 1)  
662 (16, 20) or commonness (19) based on whether they were above or below the median value in  
663 each dimension, and then use randomization tests to determine whether species of each form  
664 were observed more or less often than expected by chance (i.e., a scenario where values for  
665 each dimension are decoupled and shuffled among species so that associations among them are  
666 random; see SI Appendix, section 'Randomizations'). To ensure that results were not sensitive to  
667 the chosen cutoff, randomizations were also performed with species classified to invasiveness or  
668 commonness forms based on whether they were below the 0.25 or above the 0.75 quantile for  
669 each dimension. In order to determine whether associations among invasiveness dimensions

670 differed for species with limited native ranges within Europe or originating from completely outside  
671 Europe, we repeated these randomization tests for restricted subsets of species based on the  
672 extent of their native European distribution (57). Starting with all species, we subsequently  
673 excluded those with native distributions exceeding a threshold number of regions in Europe,  
674 moving towards a final analysis that included only extra-European aliens.  
675

#### 676 *Assessing the traits and origins of successful invaders*

677 To test specific drivers of success along each invasiveness dimension, we combined available  
678 data on species traits and their historical origins; variables included growth form, functional traits  
679 (6 traits reduced via principal component analysis to composite variables  $PC_{Size}$  and  $PC_{Econ}$ ; see  
680 SI Appendix, section 'Trait data', Table S8, Table S9, and Fig. S2) (58, 59), specialization for  
681 long-distance dispersal (100), region of origin (intra- versus extra-European) (57), and year of first  
682 record (60). Sample sizes for subsequent analyses included all species with complete data for the  
683 traits relevant to the given analysis and are reported in results tables (also see SI Appendix, Fig.  
684 S6 and S7 and Databases S1 and S2).  
685

686 To determine whether certain traits or aspects of historic origin were associated with success in  
687 each invasiveness dimension, we performed separate linear regressions with log-transformed  
688 dimension values as the response and interactions between the region of origin (intra- versus  
689 extra-European),  $PC_{Size}$ ,  $PC_{Econ}$ , and the year of first record, in addition to specializations for long-  
690 distance dispersal as explanatory variables. Growth form was also included as an explanatory  
691 variable to ensure that any potential trait relationships acted independently to the broadscale trait  
692 differences among forbs, graminoids, shrubs, and trees (see SI Appendix, Fig. S2). Interaction  
693 effects that were not significant were removed from models. We additionally analyzed these  
694 relationships using PGLS regression. For models testing for drivers of dimensions of  
695 commonness in native distributions, explanatory variables included growth form,  $PC_{Size}$ ,  $PC_{Econ}$ ,  
696 and long-distance dispersal syndrome.  
697

698 We also tested whether species attributed to each of the eight forms of invasiveness shared  
699 similar traits or historic origins. This was done using randomization tests where associated  
700 variables were shuffled among species 10,000 times (with values for the two trait PCs remaining  
701 linked). For region of origin, we analyzed all species together and for the remaining  
702 characteristics, we analyzed intra- and extra-European aliens separately to account for potential  
703 interactions. Within each form of invasiveness, we compared the observed number of species  
704 from each growth form, geographic origin category, and specialized or not for long-distance  
705 dispersal (the three dispersal syndromes were grouped for these analyses) to the expected  
706 numbers derived from randomizations. For  $PC_{Size}$ ,  $PC_{Econ}$ , and the year of first record, we  
707 compared the mean observed value within a form of invasiveness to the mean value for species  
708 assigned to that type across randomizations. Standardized difference scores (z) and significance  
709 were determined following the methods described in the SI Appendix, section 'Randomizations'.  
710

#### 711 *Assessing the habitat associations of specialist species*

712 Finally, we assessed the habitats of highest occurrence frequency for the species showing the  
713 four forms of invasiveness or commonness that are characterized by habitat specialization (form  
714 0, form A, form W, and form AW in Fig. 1). We performed randomizations, reshuffling the most  
715 frequented habitats reported among all habitat specialist forms 10,000 times, comparing the  
716 observed number for each habitat type within each form of invasiveness or commonness to the  
717 expected number derived from randomizations. Standardized difference scores (z-scores) and  
718 significance were calculated as described in the SI Appendix, section 'Randomizations'. Finally,  
719 we tested the hypothesis that for habitat-specialist species, those that are widespread (forms W  
720 and AW) are more likely to occur in habitats that cover large areas in Europe compared to  
721 restricted-range specialists (forms 0 and A). We used an ANOVA to compare the log-transformed  
722 area in Europe covered by the habitats most frequented by species in these four forms of  
723 invasiveness or commonness (Estimated areas for each habitat in Europe are reported in SI



724 Appendix, Table S18; sources and methods for obtaining these values are outlined in SI  
725 Appendix, section ‘Estimating habitat areas’).

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729

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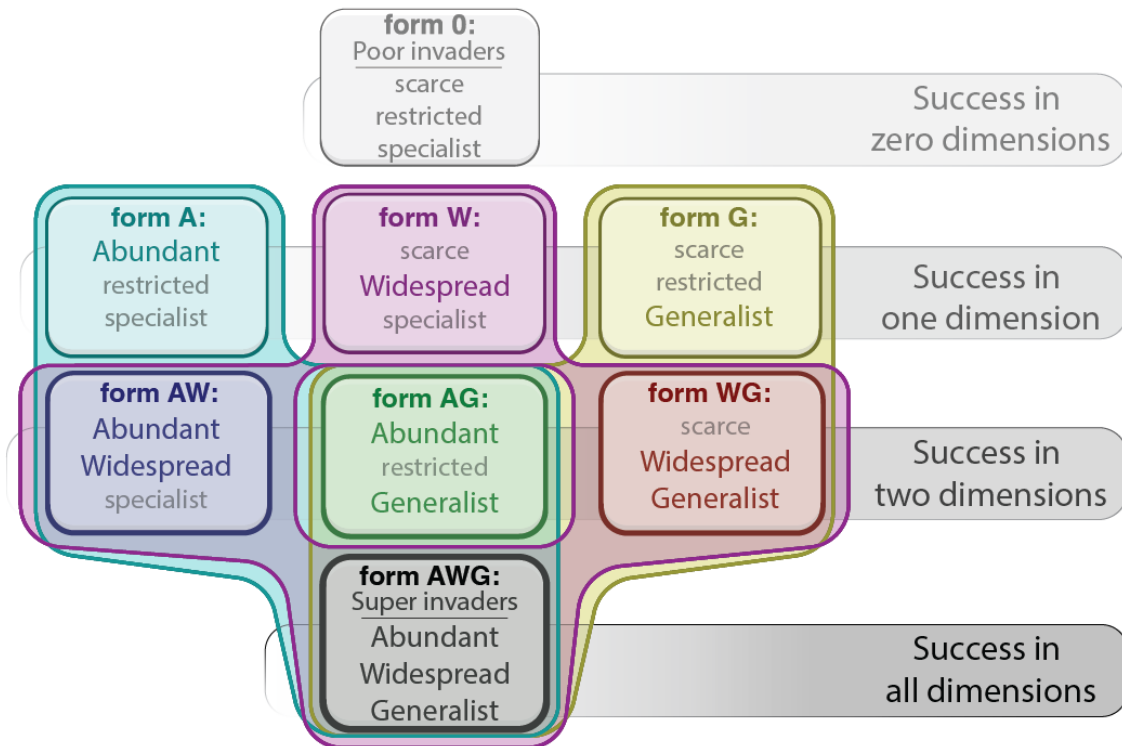
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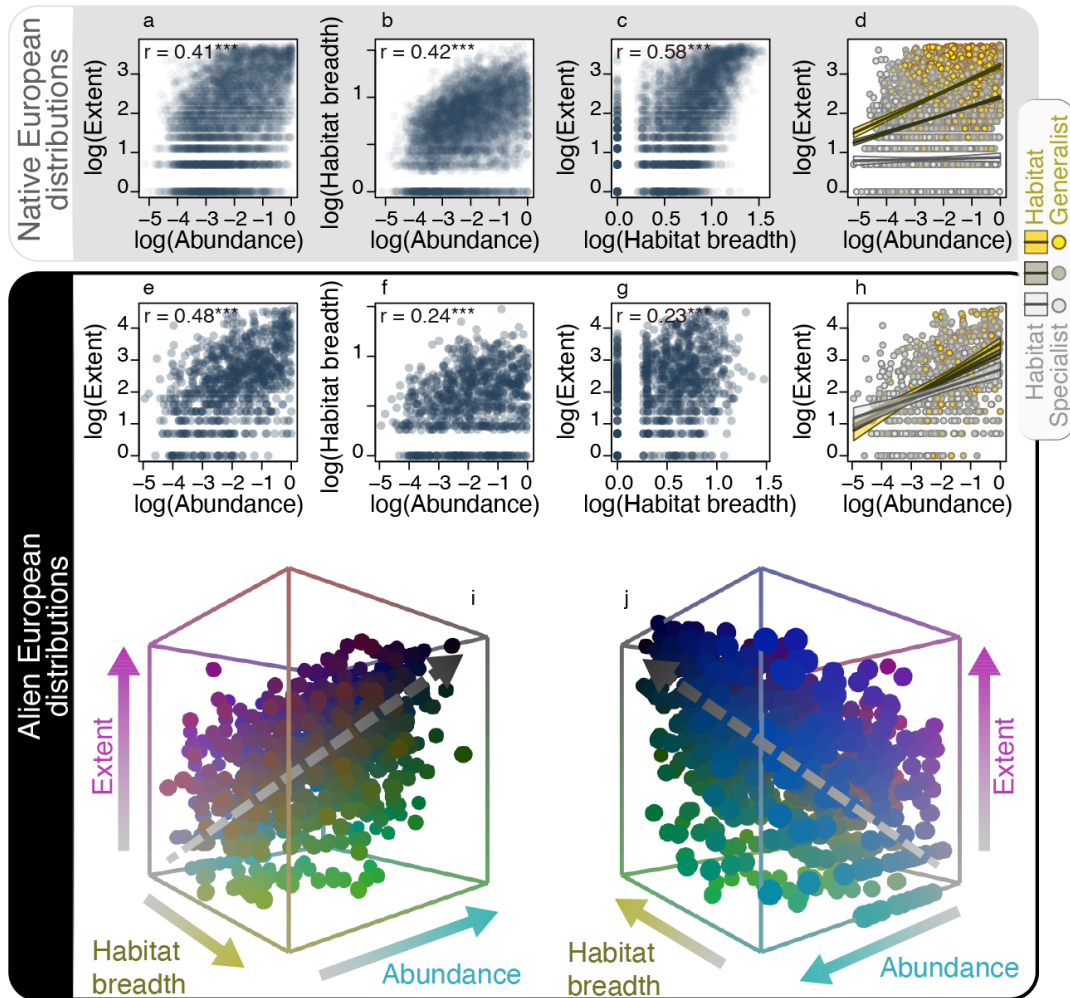




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**Figure 1.** Conceptual diagram outlining the eight different forms of invasiveness depending on success in zero, one, two, or three dimensions of invasiveness (based on (16, 18, 20)). Forms of invasiveness within the cyan polygon are associated with high naturalized abundance, within the magenta polygon with widespread naturalized geographic extent, and within the yellow polygon with high naturalized habitat breadth. Overlap between magenta and cyan is blue, between cyan and yellow is green, between magenta and yellow is red, and between all three is black. The forms of invasiveness are comparable to analogous forms of commonness used to describe species in their native distributions, and we refer to the same abbreviations in both cases.

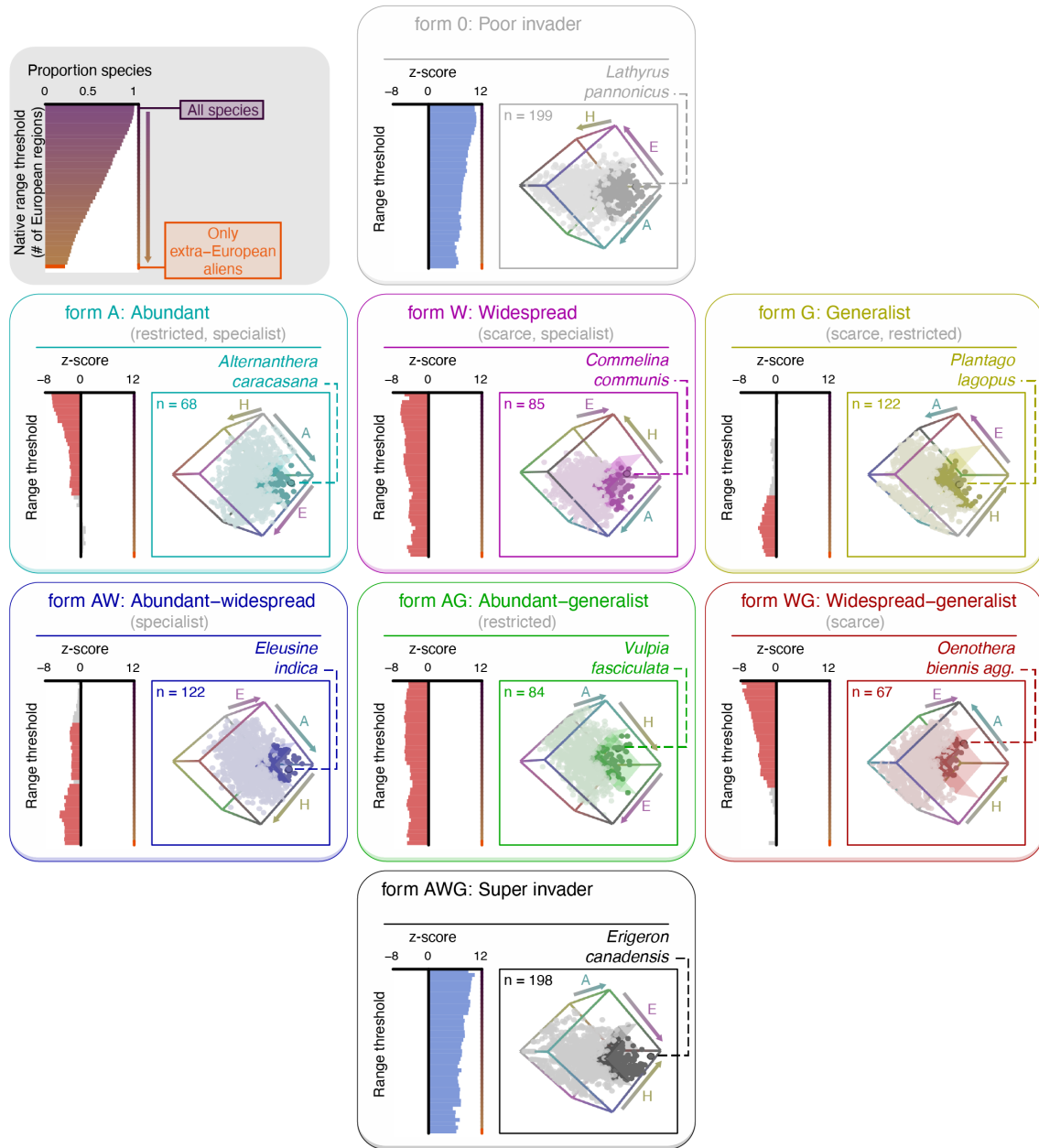
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**Figure 2.** Correlations among abundance, extent, and habitat breadth for species' native (a-d;  $n = 6052$ ) and alien (e-j;  $n = 945$ ) distributions in Europe, shown through bivariate correlations (a-c and e-f), the interacting effect of abundance and habitat breadth on extent (d and h), and species positions within 3-dimensional invasiveness space (e-f). In panels d and h, the color of points depict species habitat breadth scores (from low scores in light grey to high scores in yellow); lines and shaded areas depict the predicted fit and 95% confidence interval at the 0.1 (light grey), 0.5 (dark grey), and 0.9 (yellow) quantile of habitat breadth values. In panels i and j, the color of each point corresponds to its relative position in three dimensional invasiveness space following the color scheme outlined in figure 1 and the CMY model of color mixing (101): position along the abundance axis is associated with the amount of cyan, position along the extent axis with magenta, and position along the habitat breadth axis with yellow. The dashed diagonal arrows in panels i and j represent the hypothesized continuum from overall poor invaders (light grey) to super invaders that excel in all three dimensions (dark grey). Extent of native distributions is calculated as the number of occupied regions in the Euro+Med Plantbase and for alien distributions as the number of naturalized regions in the GloNAF database (see 'Quantifying extent' in the methods), so values cannot be directly compared between groups.

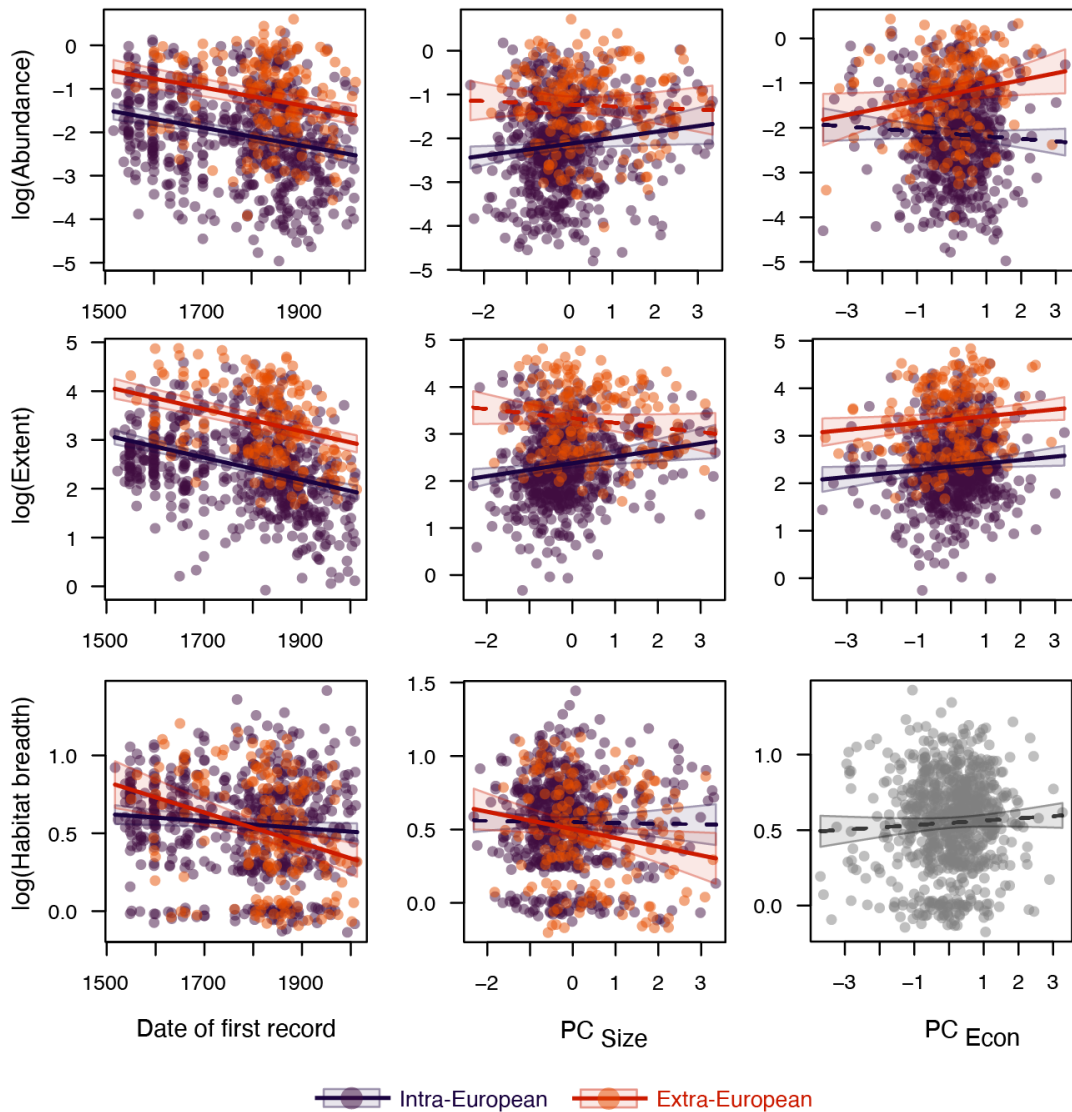
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**Figure 3.** Representation of Europe's alien flora among eight forms of invasiveness. Analyses were performed across species subsets based on the extent of their native European ranges, starting with all species (n = 945) and subsequently excluding species with native ranges exceeding a threshold number of European regions (i.e., range threshold), eventually including only extra-European aliens (n = 209); the top left panel shows the proportion of species included in each analyzed subset (see methods for more details). The vertical bar plots on the left of each of the remaining eight panels depict the results of randomization analyses: z-scores are the standardized differences between the observed number of species categorized in a given invasiveness form and the expected numbers derived from randomizations; results for the full

1019 species sample are at the top of the bar plot and those for the subset including only extra-  
1020 European aliens at the bottom). Blue bars indicate a form with significantly more species than  
1021 expected for a given species subset, red bars indicate a form with significantly fewer species, and  
1022 grey bars indicate forms where the number of species did not differ significantly from  
1023 expectations. Within each panel, the 3-dimensional invasiveness plots - with axes representing  
1024 naturalized abundance (abbreviated 'A'), geographic extent ('E'), and habitat breadth ('H') – show  
1025 how species were classified into the eight invasiveness forms based on continuous dimension  
1026 values. The species classified to the given form of invasiveness are highlighted and the area  
1027 used for classification (defined by the median value for each dimension) is delineated with semi-  
1028 transparent planes. Each invasiveness space is rotated to best show positions corresponding to  
1029 the given category, the direction of increase for each axis is shown through arrows. An example  
1030 species is highlighted in each category.  
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1036 **Figure 4.** Partial residual plots depicting the combined effects of geographic origin (i.e., intra-  
 1037 versus extra-European aliens), year of first recorded alien occurrence in Europe,  $PC_{Size}$  (low  
 1038 values: short height and low investment in stem and leaf structure; high values: tall height and  
 1039 high investment in stem and leaf structure), and  $PC_{Econ}$  (i.e., position on leaf economics spectrum;  
 1040 low values: conservative growth strategies; high values: acquisitive growth strategies) on  
 1041 abundance, geographic extent, and habitat breadth in the naturalized range ( $n = 783$ ). In panels  
 1042 where the explanatory variable was significantly associated with the given invasiveness  
 1043 dimension, the relationship for intra-European aliens is in purple and for extra-European aliens in  
 1044 orange, otherwise species from each origin are grouped and shown in grey. Significant  
 1045 relationships (determined by simple slopes analysis in the case of interactions,  $\alpha = 0.05$ ) are  
 1046 indicated with solid lines, non-significant relationships with dashed lines. Additional details of the  
 1047 principal component analysis corresponding to  $PC_{Size}$  and  $PC_{Econ}$  can be found in SI Appendix,  
 1048 Table S8 and Fig. S2; full summaries for regression models are in Table 1.

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1052 **Table 1.** Results from regression analyses of naturalized abundance, extent, and habitat breadth  
 1053 of alien species (n = 783). Reference levels of categorical variables at the intercept are forb for  
 1054 growth form and intra-European for origin. Coefficients for first record date are based on centered  
 1055 and scaled values. Non-significant interactions were removed during model selection; coefficients  
 1056 and p-values from the last model which included these terms are reported in parentheses.

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	Abundance		Extent		Habitat breadth	
	$\beta$	$p$	$\beta$	$p$	$\beta$	$p$
<b>(intercept)</b>	-2.06	<0.001	2.43	< 0.001	0.55	< 0.001
<b>Extra-European origin</b>	0.86	< 0.001	0.96	< 0.001	-0.03	0.39
<b>PC<sub>Size</sub></b>	0.14	0.02	0.14	< 0.01	-0.00	0.80
<b>Extra-European origin*PC<sub>Size</sub></b>	-0.17	0.04	-0.24	< 0.001	-0.05	0.03
<b>PC<sub>Econ</sub></b>	-0.06	0.23	0.07	0.02	0.02	0.23
<b>Extra-European origin*PC<sub>Econ</sub></b>	0.21	0.01	(0.04)	(0.52)	(-0.01)	(0.67)
<b>First record date</b>	-0.26	< 0.001	-0.29	< 0.001	-0.03	0.02
<b>Extra-European origin*First record date</b>	(-0.03)	(0.76)	(-0.13)	(0.11)	-0.10	< 0.01
<b>Epizoochorous</b>	-0.40	< 0.001	-0.17	0.06	-0.01	0.79
<b>Anemochorous</b>	0.04	0.65	-0.29	< 0.001	0.03	0.27
<b>Endozoochorous</b>	-0.31	0.04	-0.17	0.15	0.03	0.57
<b>Growth form – Graminoid</b>	0.70	< 0.001	0.05	0.61	0.08	0.04
<b>Growth form – Shrub</b>	-0.01	0.96	0.15	0.22	-0.03	0.57
<b>Growth form – Tree</b>	0.21	0.27	0.16	0.27	0.11	0.05

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 1060