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

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

invasion success | forms of rarity | distribution–abundance relationship | enemy release | leaf economic spectrum

Human socioeconomic activities are altering species' global distributions, bridging natural dispersal barriers through the accidental and intentional relocation of organisms, and opening opportunities for them to expand into new regions beyond their historic native ranges (1). The outcome of any given introduction event, however, is dependent on ecological and stochastic processes, and many introduced alien species fail to establish and persist (2, 3). Even species that do achieve persistent, self-sustaining populations (i.e., become naturalized sensu ref. 4) show varying degrees of success (i.e., invasiveness) in newly occupied regions. This has been true for natural colonization events throughout Earth's history [e.g., on islands (5, 6) and during continental biotic interchanges (7–9)] and is certainly the case for the ongoing surge of human-mediated introductions (10–12). Disentangling the factors that lead to invasion success provides an opportunity not only for anticipating and mediating future anthropogenic invasions but also for better understanding the dynamics underlying natural range expansions (13).

Quantifying a species' success in invading the alien range is complex, a fact reflected in the diverse criteria applied by different authorities when deciding whether or not to classify naturalized species as invasive (14). Recent efforts have therefore recognized that invasiveness cannot be captured by a single metric

Significance

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

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but rather encompasses multiple aspects of ecological success and impact (15, 16). Some proposed metrics, such as spread rate and socioeconomic impacts, are difficult to quantify for large numbers of species (4, 17). However, Rabinowitz's three-dimensional scheme for characterizing the rarity or commonness of species in their native distributions (18, 19) has been successfully co-opted as a valuable perspective for better understanding the success of alien species (16, 20, 21). Applied in the context of introduced species, this framework recognizes the potential for established aliens to vary along at least three demographic dimensions of invasiveness: 1) in local abundance within the naturalized range, 2) in geographic range size or extent of the naturalized range, and 3) in habitat breadth in the naturalized range (16). We subsequently distinguish these metrics as dimensions of invasiveness when measured in the naturalized distributions of alien species and dimensions of commonness when measured in species native distributions.

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

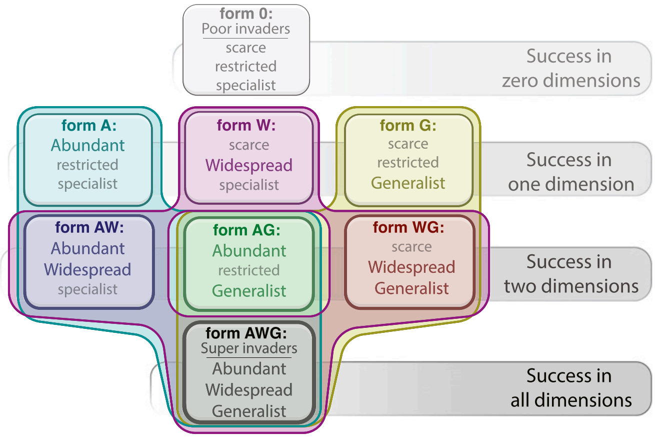

Fig. 1. Conceptual diagram outlining the eight different forms of invasiveness depending on success in zero, one, two, or three dimensions of invasiveness (based on refs. 16, 18, and 20). Forms of invasiveness within the cyan polygon are associated with high naturalized abundance, within the magenta polygon with widespread naturalized geographic extent, and within the yellow polygon with high naturalized habitat breadth. The 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.

Functional traits play a role in mediating invasion processes, but efforts to identify characteristics of successful invaders have generally resulted in few or inconsistent associations (38, 39). However, distinguishing between different components of invasiveness may provide additional clarity if each is influenced by different traits or if the same trait has contrasting effects on different dimensions (15, 16, 21, 40, 41). For example, many plant traits are associated with general trade-offs between rapid growth (i.e., acquisitive growth strategies) versus stress tolerance and survival (i.e., conservative growth strategies) (42–44), and one can hypothesize scenarios where these divergent strategies are associated with success in different dimensions of invasiveness (40, 41). Another example are specialized adaptations for long-distance dispersal that may promote rapid range expansion, both in extent and into new habitats, but likely do not provide any advantages that would influence local abundances (45, 46). For habitat specialists, their specific habitat associations may additionally be important for determining whether or not they become widespread (31).

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

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

Results

Associations among Dimensions. Bivariate correlation tests showed that all three dimensions of invasiveness were significantly positively correlated (Fig. 2 *E*–*I*). The strongest link in the naturalized distributions of alien species was between the geographic extent and local abundance dimensions ($r = 0.48$, $P < 0.001$); correlations between either of these two dimensions and the habitat breadth dimension were relatively low but significant (abundance-habitat breadth: $r = 0.24$, $P < 0.001$; extent-habitat breadth: $r = 0.23$, $P < 0.001$). Patterns were very similar for dimensions of commonness in native European distributions (including from the native distributions of intracontinental aliens), though correlations involving habitat breadth were stronger in this context (abundance–extent: $r = 0.41$, $P < 0.001$; abundance-habitat breadth: $r = 0.42$, $P < 0.001$; extent-habitat breadth: $r = 0.58$, $P < 0.001$; Fig. 2 *A*–*C*). Our results additionally suggest that correlations among dimensions increase as distributions are given time to approach equilibrium. When alien species were grouped by their year of first alien occurrence, correlations among invasiveness dimensions were strongest for the subset of species with dates prior to 1800 ($n = 326$; abundance–extent: $r = 0.51$, $P < 0.001$; abundance-habitat breadth: $r = 0.34$, $P < 0.001$; extent-habitat breadth: $r = 0.34$, $P < 0.001$), intermediate for those with dates between 1800 and 1900 ($n = 336$; abundance–extent: $r = 0.47$, $P < 0.001$; abundance-habitat breadth: $r = 0.20$, $P < 0.001$; extent-habitat breadth: $r = 0.24$, $P < 0.001$), and weakest for species introduced from 1900 onwards in which correlations between habitat breadth and the other two dimensions were not significant ($n = 174$; abundance–extent: $r = 0.37$, $P < 0.001$; abundance-habitat breadth: $r = 0.10$, $P = 0.18$; extent-habitat breadth: $r = 0.13$, $P = 0.09$). We also identified interactions in the relationships among dimensions: high abundance was more strongly associated with widespread extent for habitat generalist species than for habitat specialists in alien distributions (adjusted R^2 for interaction model = 0.25; *SI Appendix*, Table S1 and Fig. 2*H*) as well as in native distributions (adjusted $R^2 = 0.38$; *SI Appendix*, Table S2 and Fig. 2*D*). These patterns were consistent when analyzed with phylogenetic generalized least squares (PGLS) regression (*SI Appendix*, Tables S3 and S4) and for the subset of extra-European aliens (i.e., those with native distributions completely outside of the continent; *SI Appendix*, Tables S5 and S6).

The general correspondence among invasiveness dimensions is evident when visualizing all three simultaneously, with most species falling along an axis from low to high values in all three dimensions (Fig. 2 *I* and *J*). Randomization tests further revealed how the filling of this three-dimensional invasiveness space differed from null expectations (i.e., a scenario where dimensions are not correlated; Fig. 3). Poor invaders (form 0) and super invaders (form AWG) were the only invasiveness categories that

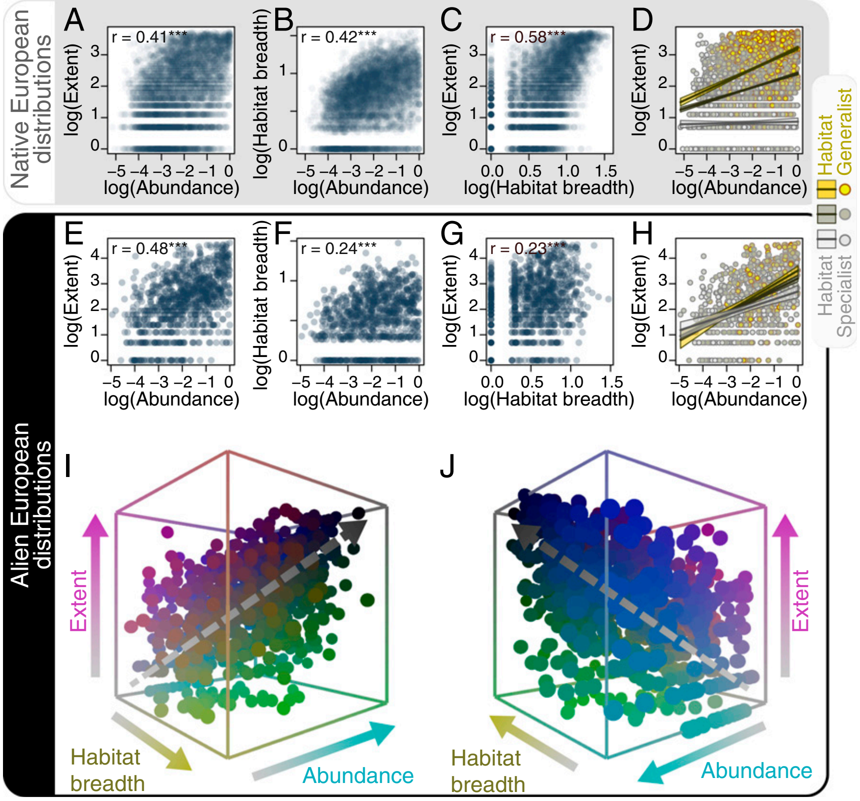

Fig. 2. Correlations among abundance, extent, and habitat breadth for species' native (*A*–*D*; $n = 6{,}052$) and alien (*E*–*J*; $n = 945$) distributions in Europe shown through bivariate correlations (*A*–*C* and *E*–*G*), the interacting effect of abundance and habitat breadth on extent (*D* and *H*), and species positions within three-dimensional invasiveness space (*I* and *J*). In *D* and *H*, the color of points depicts species habitat breadth scores (from low scores in light gray to high scores in yellow); lines and shaded areas depict the predicted fit and 95% CI at the 0.1 (light gray), 0.5 (dark gray), and 0.9 (yellow) quantile of habitat breadth values. In *I* and *J*, the color of each point corresponds to its relative position in three-dimensional invasiveness space following the color scheme outlined in Fig. 1 and the cyan, magenta, yellow model of color mixing (101): the position along the abundance axis is associated with the amount of cyan, the position along the extent axis with magenta, and the position along the habitat breadth axis with yellow. The dashed diagonal arrows in *I* and *J* represent the hypothesized continuum from overall poor invaders (light gray) to super invaders that excel in all three dimensions (dark gray). The 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 (*Quantifying Extent*), so values cannot be directly compared between groups.

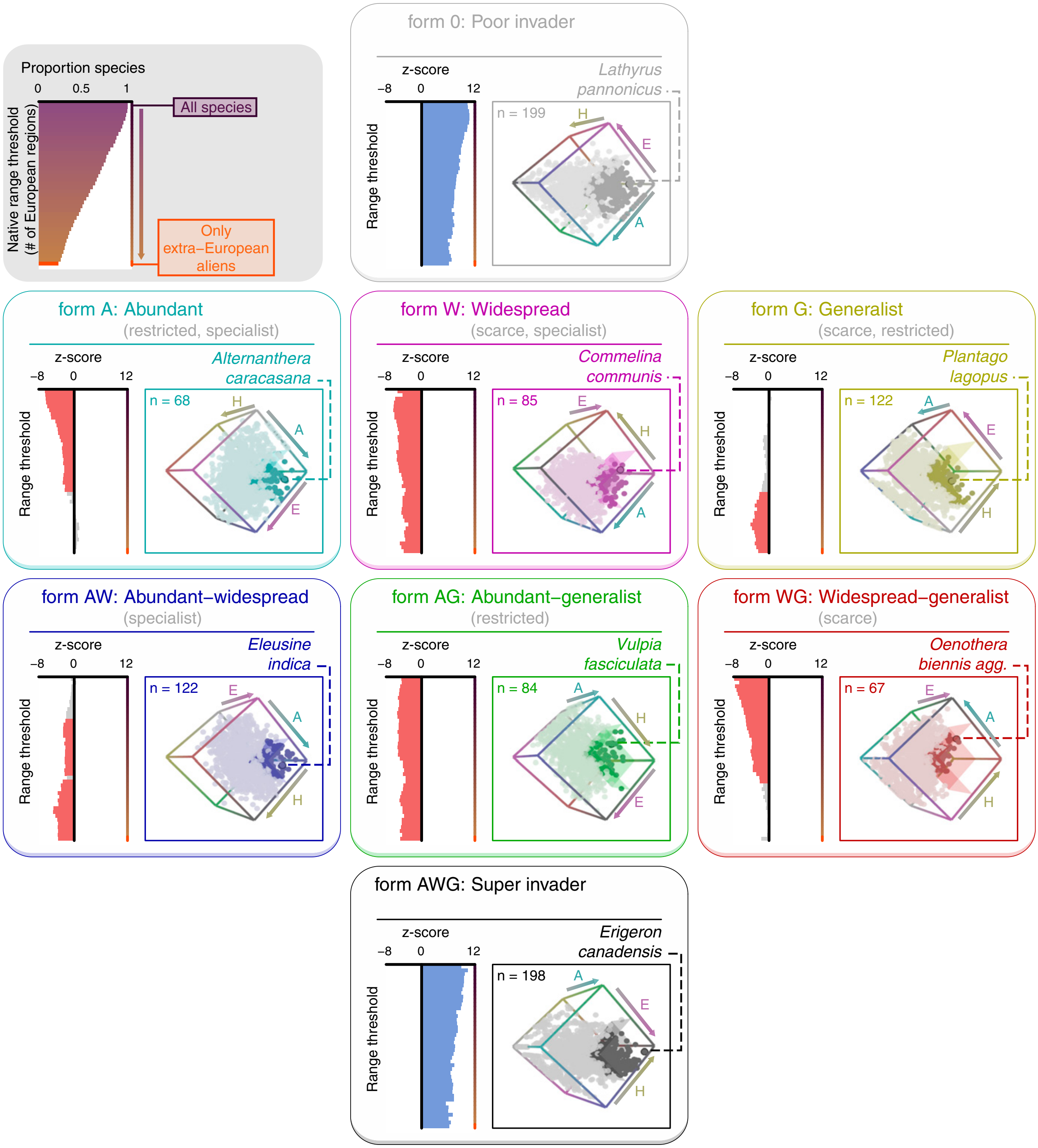

Fig. 3. Representation of Europe's alien flora among eight forms of invasiveness. Analyses were performed across species subsets based on the extent of their native European ranges, starting with all species (n = 945) and subsequently excluding species with native ranges exceeding a threshold number of European regions (i.e., range threshold), eventually including only extra-European aliens (n = 209). (*Top*, *Left*) Proportion of species included in each analyzed subset (*Materials and Methods*). 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; the results for the full species sample are at the top of the bar plot and those for the subset including only extra-European aliens at the bottom). Blue bars indicate a form with significantly more species than expected for a given species subset, red bars indicate a form with significantly fewer species, and gray bars indicate forms in which the number of species did not differ significantly from expectations. Within each panel, the three-dimensional invasiveness plots—with axes representing naturalized abundance (abbreviated "A"), geographic extent ("E"), and habitat breadth ("H")—show how species were classified into the eight invasiveness forms based on continuous dimension values. The species classified to the given form of invasiveness are highlighted, and the area used for classification (defined by the median value for each dimension) is delineated with semitransparent planes. Each invasiveness space is rotated to best show positions corresponding to the given category, and the direction of increase for each axis is shown through arrows. An example species is highlighted in each category.

included more species than expected by chance. When analyzing the full species sample, the four forms of invasiveness characterized by high abundance and low extent or vice versa (form A, form W, form AG, and form WG; Fig. 1) were significantly underrepresented. Some details in the associations among invasiveness dimensions changed as the sample of species was increasingly restricted to exclude those with widespread native distributions in Europe (eventually including only extra-European aliens). For these restricted species subsets, widespread extent showed stronger links with habitat generalism than with high abundance (i.e., form A and form WG were no longer significantly underrepresented, and form AW and form G rarely occurred). Otherwise, general patterns remained consistent across species subsets: poor and super invaders (form 0 and form AWG, respectively) were overrepresented, scarce specialist species were rarely widespread (form W was underrepresented), and abundant generalists with restricted range extents were rare (form AG was underrepresented). Similarly, in native European distributions, forms 0 and AWG were the only overrepresented forms of commonness, with over half of species categorized into one of the two (*SI Appendix*, Table. S7). All other forms of commonness were underrepresented. Results were largely consistent when the 0.25 and 0.75 quantile of each trait, rather than the median, were used to classify species into invasiveness or commonness forms (*SI Appendix*, Fig. S1 and Table S7).

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

For abundance in the naturalized range, the influence of plant height, seed mass, and investment in stem and leaf structure (together captured by principal componant $[PC]_{Size}$; *SI Appendix*, *Trait data*, Table S8, and Fig. S2) differed between intra- and extra-European aliens. Abundance increased with increasing values of PC_{Size} for intra-European aliens (simple slope: $P = 0.02$) but showed little relationship for extra-European aliens (simple slope: $P = 0.65$). This resulted in the largest differences in abundance between the two groups occurring in short-statured plants with small seeds and low investment in stem and leaf structure (Fig. 4). The position along the leaf economics spectrum (captured by PC_{Econ}; *SI Appendix*, *Trait data*, Table S8, and Fig. S2) (42, 43) also influenced naturalized abundance differently for intra- and extra-European aliens. While abundance showed a nonsignificant decrease with increasingly acquisitive growth strategies (i.e., higher PC_{Econ} values reflecting higher leaf N content, leaf area, and specific leaf area) in intra-European aliens (simple slope: $P = 0.23$), an increase in abundances was seen with increasing PC_{Econ} values in extra-European aliens (simple slope: $P = 0.03$). Overall, this gave rise to a pattern whereby abundances were highest for acquisitive species originating from outside Europe but lowest for acquisitive species introduced from within Europe (Fig. 4). Graminoids tended to occur at higher abundances and species with epizoochorous or endozoochorous long-distance dispersal syndromes tended to occur at lower abundances than species without such specializations (Table 1). Traits showed generally weak relationships with abundance in native European distributions (adjusted $R^2 = 0.11$; *SI Appendix*, Tables S9–S11); growth form was the strongest explanatory variable (additional variance explained = 0.10), being lower in forbs than in other groups.

Geographic extent of naturalized distributions was generally higher for extra-European aliens and decreased further in small-sized intra-European aliens (i.e., low PC_{Size} values; simple slope extra-European: $P = 0.14$; simple slope intra-European: $P < 0.01$; Table 1 and Fig. 4). Naturalized extent was also higher for species with acquisitive growth strategies (high PC_{Econ}), regardless of their geographic origin. Contrary to predictions, the capacity for long-distance dispersal, specifically anemochory, had a general negative effect on naturalized extent (Table 1). For geographic extent in native distributions (adjusted $R^2 = 0.10$; *SI Appendix*, Tables S9–S11), growth form was the strongest explanatory variable (additional variance explained = 0.05), being the greatest for graminoids and the smallest for shrubs. Though

Table 1. Results from regression analyses of naturalized abundance, extent, and habitat breadth of alien species ($n = 783$)

	Abundance		Extent		Habitat breadth	
	β	P	β	P	β	P
Intercept	−2.06	<0.001	2.43	<0.001	0.55	<0.001
Extra-European origin	0.86	<0.001	0.96	<0.001	−0.03	0.39
PC_{Size}	0.14	0.02	0.14	<0.01	−0.00	0.80
Extra-European origin*PC_{Size}	−0.17	0.04	−0.24	<0.001	−0.05	0.03
PC_{Econ}	−0.06	0.23	0.07	0.02	0.02	0.23
Extra-European origin*PC_{Econ}	0.21	0.01	(0.04)	(0.52)	(−0.01)	(0.67)
First record date	−0.26	<0.001	−0.29	<0.001	−0.03	0.02
Extra-European origin*First record date	(−0.03)	(0.76)	(−0.13)	(0.11)	−0.10	<0.01
Epizoochorous	−0.40	<0.001	−0.17	0.06	−0.01	0.79
Anemochorous	0.04	0.65	−0.29	<0.001	0.03	0.27
Endozoochorous	−0.31	0.04	−0.17	0.15	0.03	0.57
Growth form—Graminoid	0.70	<0.001	0.05	0.61	0.08	0.04
Growth form—Shrub	−0.01	0.96	0.15	0.22	−0.03	0.57
Growth form—Tree	0.21	0.27	0.16	0.27	0.11	0.05

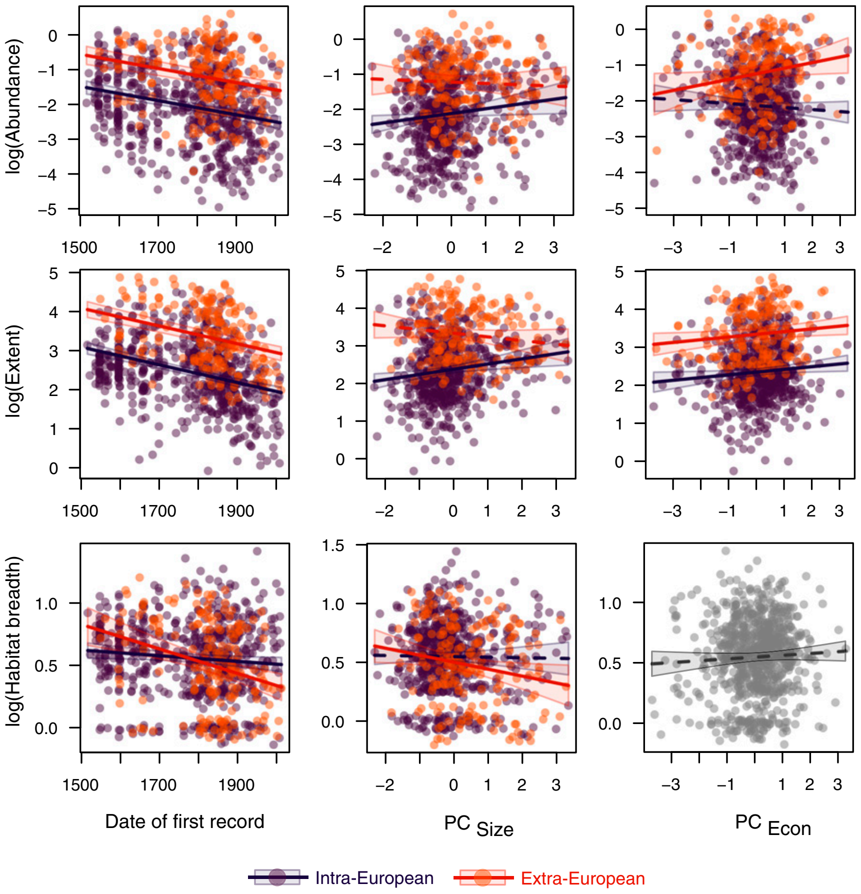

Fig. 4. Partial residual plots depicting the combined effects of geographic origin (i.e., intra- versus extra-European aliens), year of first recorded alien occurrence in Europe, $\mathrm{PC}_{\mathrm{Size}}$ (low values: short height and low investment in stem and leaf structure; high values: tall height and high investment in stem and leaf structure), and $\mathrm{PC}_{\mathrm{Econ}}$ (i.e., position on leaf economics spectrum; low values: conservative growth strategies; high values: acquisitive growth strategies) on abundance, geographic extent, and habitat breadth in the naturalized range ($n = 783$). In panels where the explanatory variable was significantly associated with the given invasiveness dimension, the relationship for intra-European aliens is in purple and for extra-European aliens in orange, otherwise species from each origin are grouped and shown in gray. Significant relationships (determined by simple slopes analysis in the case of interactions, $\alpha = 0.05$) are indicated with solid lines, and nonsignificant relationships with dashed lines. Additional details of the principal component analysis corresponding to $\mathrm{PC}_{\mathrm{Size}}$ and $\mathrm{PC}_{\mathrm{Econ}}$ can be found in *SI Appendix*, Table S8 and Fig. S2; full summaries for regression models are in Table 1.

we additionally detected weak, but significant, negative effects of $\mathrm{PC}_{\mathrm{Size}}$ and positive effects for $\mathrm{PC}_{\mathrm{Econ}}$ and seed dispersal through endozoochory.

Habitat breadth in naturalized distributions was generally higher for graminoids and for trees but after accounting for this effect, decreased with $\mathrm{PC}_{\mathrm{Size}}$ in extra-European aliens (simple slope extra-European: $P = 0.02$; simple slope intra-European: $P = 0.80$; Table 1 and Fig. 4). As was the case in naturalized distributions, traits were generally poor predictors of habitat breadth in native distributions (adjusted $R^2 = 0.03$; *SI Appendix*, Tables S9–S11). Patterns for all three invasiveness dimensions were generally similar when data were analyzed with PGLS regression, though some trait effects were no longer significant ($\mathrm{PC}_{\mathrm{Size}}$-origin interaction on naturalized abundance: $P = 0.06$; $\mathrm{PC}_{\mathrm{Exon}}$-origin interaction for naturalized abundance: $P = 0.12$; $\mathrm{PC}_{\mathrm{Econ}}$ for naturalized extent: $P = 0.07$; $\mathrm{PC}_{\mathrm{Size}}$-origin interaction for naturalized habitat breadth: $P = 0.06$; *SI Appendix*, Table S12).

Characteristics of Different Forms of Invasiveness. In addition to identifying conditions associated with each individual dimension of invasiveness, we found general patterns in the characteristics of alien species within each of the eight forms of invasiveness (*SI Appendix*, Fig. S3 and Tables S13–S17 for full results of randomization tests). Poor invaders (form 0) and restricted range generalists (form G and form AG) overwhelmingly comprised intra-European aliens. In contrast, super invaders (form AWG) and abundant, widespread specialists (form AW) were disproportionately composed of extra-European aliens (*SI Appendix*, Fig. S3 and Table S13). Species that excelled only in the abundance dimension (form A) tended toward conservative growth strategies (low $\mathrm{PC}_{\mathrm{Econ}}$), regardless of origin. Otherwise, for intra-European aliens, habitat generalist species that were also abundant (form AG and form AWG) tended to be larger in size (high $\mathrm{PC}_{\mathrm{Size}}$); poor invaders (form 0) and species that excelled in only the habitat breadth or abundance dimensions (form G and form A) were smaller (low $\mathrm{PC}_{\mathrm{Size}}$), and widespread generalists tended toward acquisitive growth strategies (high $\mathrm{PC}_{\mathrm{Econ}}$; *SI Appendix*, Table S14). Differences in growth forms among forms of invasiveness were largely consistent with the results for $\mathrm{PC}_{\mathrm{Size}}$ and $\mathrm{PC}_{\mathrm{Econ}}$ (*SI Appendix*, Table S15).

All eight forms of invasiveness included species with dates of first alien occurrence ranging from at least the mid-16th century to the turn of the 21st century (*SI Appendix*, Fig. S3). However, super invaders (form AWG) and intra-European aliens classified in form WG were associated with earlier recorded dates of introduction in Europe (*SI Appendix*, Fig. S3 and Table S16). In contrast, poor invaders (form 0), species that succeeded in only the habitat breadth or the abundance dimensions (form G and form A), were associated with relatively recent dates of introductions. Species specialized for long-distance dispersal did not show any strong patterns besides the overrepresentation of specialized dispersers among extra-European aliens classified as overall poor invaders (form 0) and their underrepresentation among form AW species (*SI Appendix*, Table S17).

Habitats of Specialists. We found that, on average, the habitats occupied by species that were habitat specialists in their naturalized distributions (invasiveness form 0, form A, form W, and form AW) differed in area of coverage across Europe (F = 2.71, $P = 0.04$; *SI Appendix*, Fig. S4 *A* and *B*). Specifically, alien species in form AW occurred in the most widespread habitats, though differences were small, variation was high, and this group was only statistically distinguishable from poor invaders (form 0; Tukey honest significant difference test: $P = 0.05$). Form AW alien species also showed a strong association with ruderal habitats; this was the only habitat where either invasiveness form of widespread habitat specialists (form W or AW) were overrepresented (*SI Appendix*, Fig. S4*C*). In native distributions, widespread habitat specialists also occurred in more widespread habitats (F = 10.89, $P < 0.001$; *SI Appendix*, Fig. S5 *A* and *B*). Abundant habitat specialists with restricted ranges (form A) in particular occurred in habitats with limited area in Europe. Notably, habitat specialists that were widespread in their native European distributions (form W and form AW) were overrepresented in cropland habitats, the most widespread habitat in Europe, while those that also reached high abundances (form AW) were additionally overrepresented in ruderal habitats (*SI Appendix*, Fig. S5*C*).

Discussion

Our analysis of multidimensional invasion success in Europe's alien flora demonstrates that local abundance, range extent, and habitat breadth of naturalized distributions are positively associated at the continental scale. Most species fall along a spectrum from overall poor invaders to super invaders that excel in all three dimensions. These results echo patterns that we found for the dimensions of commonness measured from the distributions of native European flora and that have been previously documented in the native distributions of various taxa (23–26, 33). This suggests that similar mechanisms structure alien and native distributions at macroecological scales. Our finding of positive associations between abundance and geographic extent in the distributions of both native and alien species may seem at odds with a recent study that found low support for similar correlations in native European flora (34). However, this apparent discrepancy can be explained by our use of maximum abundance as a proxy of potential for local dominance (16, 61, 62) rather than averaging abundances across the entire range. This is consistent with previous studies that have found stronger abundance–extent relationships when using measures of maximum abundance (63). For alien distributions, our results largely correspond with those from a regional assessment of French grassland communities (20) but contrast with findings from Southeast Australia (16), perhaps reflecting that species introductions in Oceania have primarily occurred more recently, and aliens there may not have had the necessary time to expand along each dimension (60). Indeed, our results suggest that many alien distributions have not reached equilibrium (37). Correlations among invasiveness dimensions were strongest for plant species with earlier dates of introduction, indicating that deviations from general patterns are at least partially driven by time lags in invasion processes (35, 36). In addition to earlier dates of introduction, extracontinental origins were associated with higher performance along all three dimensions of invasiveness. Species functional traits, on the other hand, were typically poor predictors of dimensions in both alien and native distributions. This is perhaps unsurprising considering the diversity of successful ecological and life history strategies that can be observed within and across natural systems (64). Nevertheless, we did find a number of significant trait effects, often showing interactions within the context of alien species' geographic origins, that are in line with hypothesized mechanisms of invasion (see text below). Taken together, our analyses identified characteristics of species and their introduction histories that help to explain why they showed success in only one, two, or in all three dimensions.

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

Our results, however, suggest that investment in rapid growth may be one path for aliens to become widespread without necessarily reaching high abundances locally. Acquisitive traits have been associated with range filling in native distributions (46), and we found that high values of trait $\mathrm{PC}_{\mathrm{Econ}}$, indicating acquisitive growth strategies, were associated with larger extents for native and naturalized ranges. However, we found that intracontinental aliens with these traits showed lower naturalized abundance and were overrepresented among the relatively few generalist species that were locally scarce but widespread in their naturalized distributions (*SI Appendix*, Fig. S3). In contrast, locally abundant species with restricted naturalized ranges tended to show conservative growth strategies. However, we found that many of the forms of invasiveness characterized by restricted geographic extent were associated with more recent introductions, suggesting that these patterns are influenced by time lags in invasion processes and that some of these species are likely to continue to expand their ranges in the future (35). This is potentially true even for species that currently appear to be overall poor invaders, and notice should be taken if they begin to increase in any of the three dimensions.

We predicted that alien species with diaspores adapted to long-distance dispersal should have broader naturalized extents. A rather modest increase in the extent for endozoochorous species indicates that this may be the case for native distributions, but we found the opposite pattern for alien distributions, particularly for anemochorous aliens. Some potential reasons are that alien plants might be mostly dispersed by anthropogenic vectors, via many short-distance stepwise dispersal events (e.g., clonal spread, myrmecochory, barochory) or through stochastic events or other vectors for which long-distance dispersal syndromes have a negligible, or even negative, effect (71, 72). For epizoochorous and endozoochorous aliens, specialized diaspores were also associated with lower naturalized abundances, suggesting that these adaptations may aid in the rapid colonization of newly available sites but decrease establishment success [e.g., fugitive species concept (73)]. Plant height, on the other hand, is also associated with dispersal ability and establishment success and was positively associated with naturalized extent in intra-European aliens (74, 75).

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

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

We found that the difference in abundance between intra- and extra-European aliens was dependent on traits that mark a general trade-off between rapid growth and increased survival, consistent with expectations of the enemy release hypothesis (51). Acquisitive growth strategists are particularly vulnerable to pathogens, herbivores, and competitors (84–86), suggesting a higher potential to benefit from enemy release (87, 88), but escape from biotic constraints is less likely when species are introduced to areas near their native distributions. Indeed, while acquisitive species introduced from outside of Europe were generally the most abundant and widespread aliens, we found that those originating from within the continent were typically scarce where naturalized. Larger species that invest in stem and leaf structure (high PC_{Size}) and conservative growth strategies (low PC_{Econ})—traits associated with increased resistance to biotic enemies (84–86, 89)—tended to reach intermediate abundances whether they originated from inside or outside Europe. Unburdened from biotic constraints and capable of rapid growth, acquisitive extra-European aliens may be particularly suited for outcompeting native species and other aliens in disturbed habitats where the availabilities of resources such as light or nitrogen tend to be higher. As human activities continue to alter natural landscapes, we should therefore expect these species to find increasing success as invaders into the future (90, 91).

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

Materials and Methods

Flow diagrams illustrating the databases and analyses used in this study are provided in *SI Appendix*, Figs. S6 and S7. Data and R code used for analyses can be found in Datasets S1–S6.

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

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

Quantifying Habitat Breadth. Each EVA survey plot was assigned to one of 229 habitat types of the European Nature Information System (EUNIS) using the classification expert system EUNIS-ESy version 2020–06-08 (95). These habitat types were further merged into 47 broader habitat types used in this study (*SI Appendix*, Table S18). Habitat classification was possible for 66% of the nearly 390,000 EVA plots that included aliens and 60% of over 1.2 million plots that included native species; these were used to quantify the habitat breadth of species naturalized and native ranges, respectively. Because not all habitat types are equally distinct (e.g., wet and mesic grasslands are more similar to each other than either is to taiga), our measure of habitat breadth accounts for floral similarity among habitats by calculating the effective habitat number for each species following the method in ref. 96 (*SI Appendix*, *Effective habitat number* and Fig. S9). In addition to calculating habitat breadth, we determined the habitat where each species most frequently occurred by aggregating EVA plots in 1° × 1° grid cells and counting the number of grid cells where each species was observed in each habitat.

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

The third approach was to classify species into the eight different forms of invasiveness (Fig. 1) (16, 20) or commonness (19) based on whether they were above or below the median value in each dimension and then use randomization tests to determine whether species of each form were observed more or less often than expected by chance (i.e., a scenario where values for each dimension are decoupled and shuffled among species so that associations among them are random; *SI Appendix*, *Randomizations*). To ensure that results were not sensitive to the chosen cutoff, randomizations were also performed with species classified to invasiveness or commonness forms based on whether they were below the 0.25 or above the 0.75 quantile for each dimension. In order to determine whether associations among invasiveness dimensions differed for species with limited native ranges within Europe or originating from completely outside Europe, we repeated these randomization tests for restricted subsets of species based on the extent of their native European distribution (57). Starting with all species, we subsequently excluded those with native distributions exceeding a threshold number of regions in Europe, moving toward a final analysis that included only extra-European aliens.

Assessing the Traits and Origins of Successful Invaders. To test specific drivers of success along each invasiveness dimension, we combined available data on species traits and their historical origins; variables included growth form, functional traits (six traits reduced via principal component analysis to composite variables PC_{Size} and PC_{Econ}; *SI Appendix*, *Trait data*, Tables S8 and S9, and Fig. S2) (58, 59), specialization for long-distance dispersal (100), region of origin (intra- versus extra-European) (57), and year of first record (60). Sample sizes for subsequent analyses included all species with complete data for the traits relevant to the given analysis and are reported in results tables (also see *SI Appendix*, Figs. S6 and S7 and Datasets S1 and S2).

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

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

Assessing the Habitat Associations of Specialist Species. Finally, we assessed the habitats of highest occurrence frequency for the species showing the four forms of invasiveness or commonness that are characterized by habitat specialization (form 0, form A, form W, and form AW in Fig. 1). We performed randomizations, reshuffling the most frequented habitats reported among all habitat specialist forms 10,000 times, comparing the observed number for each habitat type within each form of invasiveness or commonness to the expected number derived from randomizations. Standardized difference scores (z-scores) and significance were calculated as described in *SI Appendix*, *Randomizations*. Finally, we tested the hypothesis that for habitat specialist species, those that are widespread (forms W and AW) are more likely to occur in habitats that cover large areas in Europe compared to restricted range specialists (forms 0 and A). We used an ANOVA to compare the log-transformed area in Europe covered by the habitats most frequented by species in these four forms of invasiveness or commonness (estimated areas for each habitat in Europe are reported in *SI Appendix*, Table S18; sources and methods for obtaining these values are outlined in *SI Appendix*, *Estimating habitat areas*).

Data Availability. All study data are included in the article and/or supporting information.

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