



ECOLOGY

The poleward naturalization of intracontinental alien plants

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Plant introductions outside their native ranges by humans have led to substantial ecological consequences. While we have gained considerable knowledge about intercontinental introductions, the distribution and determinants of intracontinental aliens remain poorly understood. Here, we studied naturalized (i.e., self-sustaining) intracontinental aliens using native and alien floras of 243 mainland regions in North America, South America, Europe, and Australia. We revealed that 4510 plant species had intracontinental origins, accounting for 3.9% of all plant species and 56.7% of all naturalized species in these continents. In North America and Europe, the numbers of intracontinental aliens peaked at mid-latitudes, while the proportion peaked at high latitudes in Europe. Notably, we found predominant poleward naturalization, primarily due to larger native species pools in low-latitudes. Geographic and climatic distances constrained the naturalization of intracontinental aliens in Australia, Europe, and North America, but not in South America. These findings suggest that poleward naturalizations will accelerate, as high latitudes become suitable for more plant species due to climate change.

INTRODUCTION

Since the start of the early modern period (i.e., since ca. 1500 CE), the expansion of colonialism and trade have resulted in the introduction of tens of thousands of organisms from their native to foreign lands. Many of these species have subsequently established self-sustaining populations outside their native ranges, known as naturalized alien species (1–3). Textbook examples such as the kudzu vine (4) and the European rabbit (5) demonstrate the ecological and socioeconomic damages caused by intercontinental introductions (6, 7). However, both species have also been introduced by humans to other regions within their native continents, yet these intracontinental introductions and subsequent naturalizations have generally received less attention (8). This arises from a historical view that intracontinental aliens are less common and less problematic than intercontinental aliens (9, 10). However, recent studies challenge this view, revealing that intracontinental aliens are common (11), and some of them have become problematic (9,

12). For example, over half of the naturalized alien plants in Europe have an intracontinental origin (13). Moreover, the accumulation of intracontinental aliens shows no sign of saturation, especially with climate change causing some of the regions to become increasingly suitable for species from warmer regions (14, 15). Still, a global assessment of the distribution of intracontinental aliens and the underlying determinants is lacking.

As native species diversity generally declines from the equator to the poles (16, 17), there is a larger pool of species that could be introduced toward the poles compared to the opposite direction. Therefore, we expect that intracontinental aliens will predominantly naturalize toward the poles. However, naturalization of intracontinental aliens is also likely to be assisted by anthropogenic effects (18) and to be constrained by biogeographic factors that broadly fall within the three categories of the BAM framework: Biotic, Abiotic (climatic), and Movement (geographic). Climatic suitability is probably the most widely considered environmental filter (19), and its importance has received strong empirical support (20, 21). As the number of naturalized alien plants has strongly increased during the last century (1), we expect that rapid climatic change during the last decades has enabled even more low-latitude species to naturalize at higher latitudes than expected from the native species richness gradient alone. Furthermore, a recent study revealed that alien birds were more likely to naturalize to regions that have bird communities similar to those in their native regions, suggesting that biotic distance can also constrain naturalization (22). In addition, naturalization can be constrained by geographic distance and physical barriers. Although humans have helped naturalized alien species overcome these barriers (23), the probability of introduction by human-assisted movements of species is likely to be higher between nearby regions than between distant ones (24). Understanding the interplay among these factors in shaping the latitudinal patterns of intracontinental naturalization

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is therefore crucial for predicting and controlling the future spread of alien species.

Here, we assess latitudinal patterns of naturalization for 4510 intracontinental alien plant species across 243 administrative regions (e.g., countries or federal states) spanning four continents, i.e., North America, South America, Europe, and Australia, by combining regional lists of native (25) and naturalized alien (26) flowering plant species. Note that our study focuses on species introduced by humans, which means that it does not include unassisted range expanders—native species that actively expand their range without direct human assistance (15). We investigate the absolute numbers of intracontinental alien plants and their proportions relative to all naturalized species (also including intercontinental aliens) across regions and latitudes and assess their latitudinal shifts as the latitudinal distances between native (donor) and naturalized (recipient) regions (Fig. 1A). We identify the determinants underlying the naturalization of intracontinental aliens by comparing observed patterns of latitudinal shifts to patterns predicted by models based on the anthropogenic effect and the climatic, biotic, and geographic distances between the recipient and donor regions (Fig. 1, B and C).

RESULTS

Numbers and proportions of intracontinental aliens

We found that intracontinental aliens were prevalent. Over the 243 regions (~38% of the global ice-free land surface) across the four continents considered, 4510 flowering plant species had intracontinental origins, accounting for 3.9% of all plant species and 56.7% of all naturalized plant species. North America had the largest number of intracontinental aliens ($n = 2645$; Fig. 2A), followed by Europe ($n = 1603$), South America ($n = 603$), and Australia ($n = 457$).

Generalized additive mixed-effect models (GAMMs) showed that while the area-corrected number of intracontinental aliens did not strongly change with latitude in the Southern Hemisphere, it peaked at around 40° in the Northern Hemisphere (edf = 4.89, $F = 17.7$, $P < 0.001$; Fig. 2B). Intracontinental aliens as a proportion of all naturalized aliens (also including intercontinental ones) were highest in Europe (64.5%; Fig. 2C), followed by North America (45.5%), South America (38.1%), and Australia (15.6%). The GAMMs showed that while the proportion of intracontinental aliens to all aliens decreased with latitude in the Southern Hemisphere, it slightly increased with latitude in the Northern Hemisphere, particularly in Europe (edf = 6.14, $F = 35.6$, $P < 0.001$; Fig. 2D). Intracontinental aliens as a proportion of all species (including both natives and aliens) were highest in Europe (8.9%), followed by North America (7.3%), Australia (2.7%), and South America (0.8%). The GAMMs showed that the proportion of intracontinental aliens to all species peaked at around 50° in both hemispheres (edf = 8.33, $F = 37.1$, $P < 0.001$; fig. S1).

Latitudinal shifts of intracontinental aliens

Across the four continents, intracontinental aliens naturalized toward higher latitudes (i.e., regions that were closer to the poles). This is indicated by the finding that 66.1% of the regions received more species from lower latitudes than from higher latitudes (Fig. 3). This pattern holds for most regions of Europe (60.7%) and South America (72.5%) and is especially strong in North America (94.1%). However, in Australia, only 33.8% of the regions received more species from lower latitudes than from higher latitudes. Overall, intracontinental aliens naturalized toward higher latitudes by a median of 5.20 latitudinal degrees [bias-corrected 95% confidence interval (CI) of median: [2.46, 6.86]]. This value is 10.24 (95% CI: [9.00, 12.30]) in North

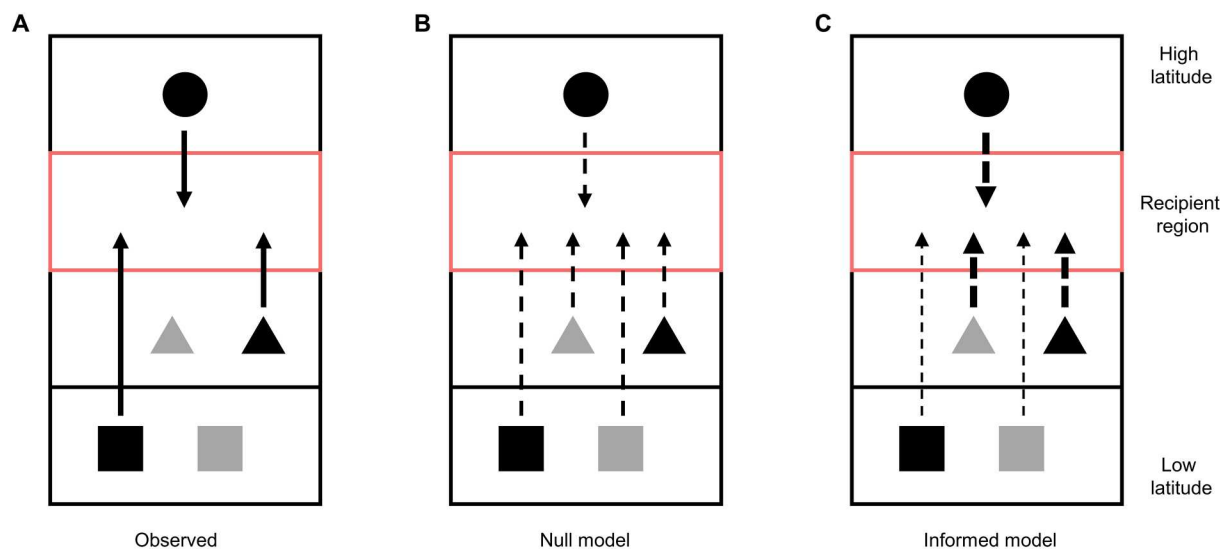


Fig. 1. Conceptual illustration of observed and predicted latitudinal shifts of intracontinental aliens. (A) Consider a hypothetical continent that contains four regions. Three species (the black symbols) that are native to the three black-rimmed donor regions have naturalized in the red-rimmed recipient region, where they are intracontinental aliens (gray symbols indicate species that have not naturalized beyond their native regions). The median latitudinal shifts of these three species reveal a trend of poleward naturalization. (B) In a null model of random naturalization, species native to the three donor regions are randomly drawn as naturalized species for the recipient region. (C) In an informed model, the probability of a species being drawn is weighted by certain anthropogenic, geographic, biotic, or abiotic predictors or a combination thereof. Here, taking the model informed by geographic distance as an example, the probability of a species being drawn decreases (as indicated by the thinner lines) with distance between its donor region and the recipient region.

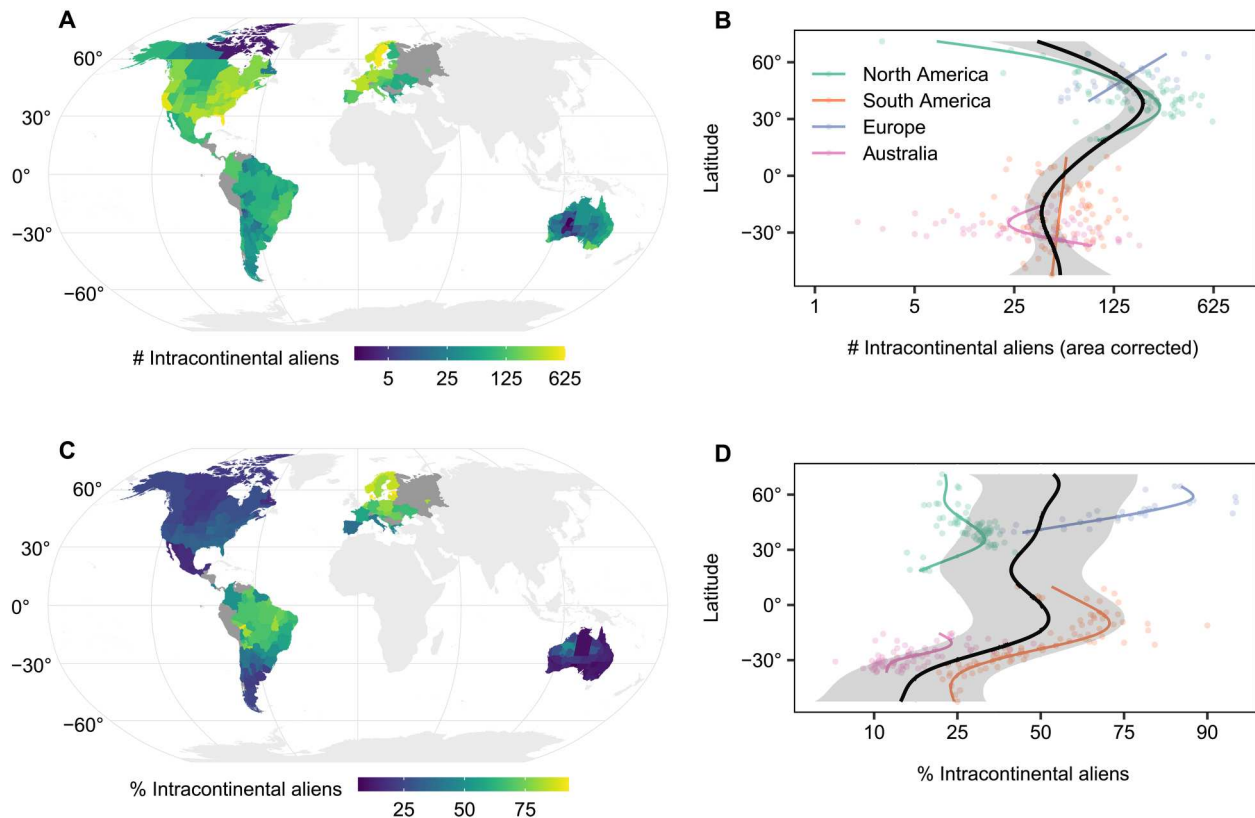


Fig. 2. Naturalized intracontinental alien plants in the four focal continents. The number of intracontinental aliens (A) and its relationship with latitude (B) across 243 regions. The intracontinental aliens as proportion of all aliens (C) and its relationship with latitude (D). In (A) and (C), dark gray color indicates regions within the four focal continents lacking data, and light gray indicates regions not included in the present study (e.g., Africa). In (B) and (D), black lines represent the general trends across all four focal continents, with the shaded area representing 95% CIs. Colored lines represent trends within each of the four continents. The lines were fitted using GAMMs. In (B), the number of intracontinental aliens was natural log-transformed and then area-corrected to account for variation in size of the regions.

America, 11.04 (95% CI: [6.11, 13.09]) in South America, and 2.18 (95% CI: [−3.56, 5.20]) in Europe. However, in Australia, intracontinental aliens naturalized toward lower latitudes by 1.90 latitudinal degrees (95% CI: [0.73, 3.27]).

Predicting latitudinal shifts of intracontinental aliens

Our null model that randomly drew native species to a given recipient region predicted the observed latitudinal shifts reasonably well. Specifically, although the null model predicted stronger poleward naturalization than observed (Fig. 3B and table S1), its overall accuracy was 87.1, 89.1, 85.1, and 87.0% for regions in North America, South America, Europe, and Australia, respectively (Fig. 4). Because of the latitudinal diversity gradient (LDG; i.e., native species diversity decreases from lower to higher latitudes; fig. S2), species from lower latitudes were more likely to be drawn in the null model. To explicitly test this LDG effect, we additionally ran a model that counteracts the LDG (anti-LDG model; see Methods). This model predicted less poleward naturalization than observed except for Australia (Fig. 3B and table S1). Moreover, it was substantially outperformed by the null model in all continents (table S2), with reduced accuracies of 22.7, 17.0, 8.6, and 16.2% for North America, South America, Europe, and Australia, respectively (Fig. 4).

We next ran 10 informed models (Fig. 1C), in which the probability of a species being drawn increased with gross domestic product (GDP) per capita (anthropogenic effect) of its donor region, decreased with geographic, climatic, or biotic distance (i.e., compositional dissimilarity based on native species) between its donor and recipient regions, or was codetermined by two of the four factors. In South America, none of the informed models outperformed the null model, which already had a very high predictive accuracy (Fig. 4). However, for the three other continents, most informed models outperformed the null models with eight, three, and four informed models outperforming the null models for North America, Europe, and Australia, respectively (Fig. 4 and table S2). Specifically, although models that were informed by the anthropogenic effect (GDP per capita) alone did not outperform the null model, models that were informed by geographic or climatic distance consistently outperformed the null models in all three continents. Furthermore, the model informed by geographic ($Z = 2.81$, $P = 0.011$) or climatic distance ($Z = 3.47$, $P = 0.002$) outperformed the average of the other informed models in Europe. The model informed by climatic distance ($Z = 3.60$, $P = 0.001$) or by both climatic and geographic distances ($Z = 2.48$, $P = 0.020$) outperformed the average of the other informed models in Australia.

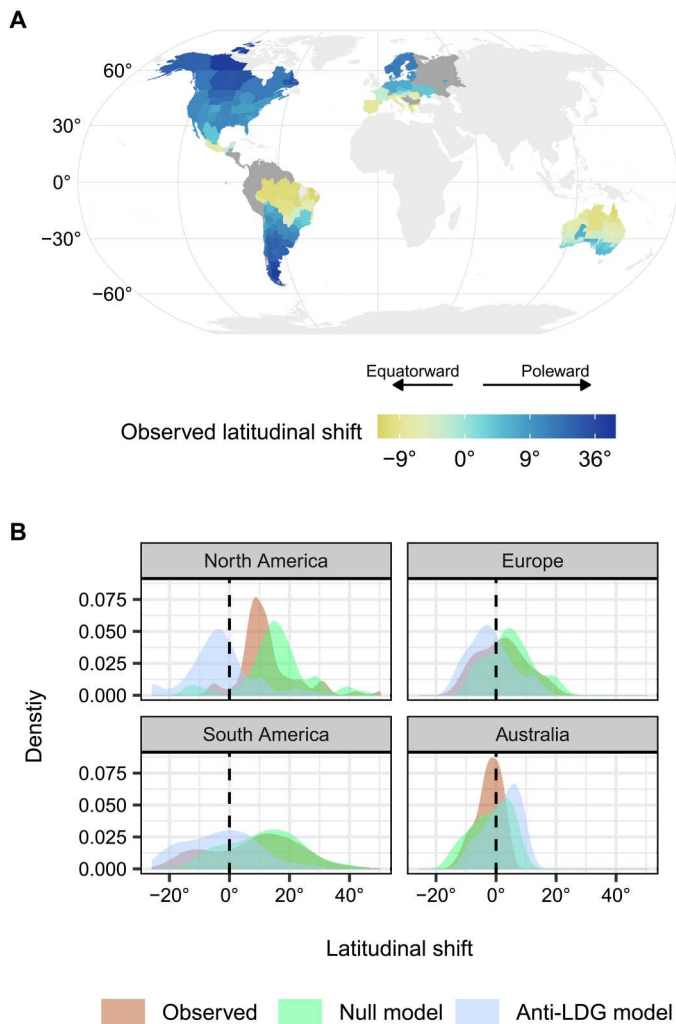


Fig. 3. Observed and predicted latitudinal shifts of intracontinental alien plants in the four focal continents. For each of the 243 recipient regions, the median latitudinal shifts of its naturalized intracontinental aliens were calculated. In (A), blue shades indicate regions that receive more intracontinental aliens from lower latitudes than from higher latitudes (i.e., intracontinental aliens naturalized toward higher latitudes), while yellow shades indicate the opposite. (B) Distribution of observed and predicted latitudinal shifts. The prediction is based on a null model where intracontinental aliens in a recipient region were randomly drawn (naturalized) from the other regions or on an “anti-LDG” model that counteracts the latitudinal diversity gradient (LDG) in native species (e.g., low and high latitudes contribute equally to species naturalization despite their difference in native species diversity; see Methods). South American regions that are located north of the equator were not included in the analysis.

DISCUSSION

By combining two of the largest databases on distributions of native (25) and naturalized alien (26) plant species, we provide a large picture of the distribution and latitudinal shifts of intracontinental aliens for four continents. Our study revealed the prevalence of intracontinental alien plants globally. Across the 243 regions included in our study, we identified 4510 naturalized alien plant species that had intracontinental origins, accounting for 3.4% of all plant species and 56.7% of all naturalized plant species. The number of intracontinental aliens peaked at mid-latitudes (around 40°) in the Northern

Hemisphere, whereas there was no clear latitudinal pattern in the Southern Hemisphere. However, the proportion of intracontinental aliens among all aliens peaked at low latitudes in the Southern Hemisphere and at high latitudes in the Northern Hemisphere, particularly in Europe. We further revealed that because the larger native species pools toward the equator than toward the poles, intracontinental aliens mainly naturalized from low- to high-latitude regions (i.e., poleward). The exception is Australia, where the latitudinal species-richness gradient is reversed. Last, while patterns of latitudinal shifts for intracontinental aliens was well predicted by a model of random naturalization (i.e., our null model) in South America, latitudinal shifts in the other three continents were even better predicted by models that considered climatic distance.

Invasion science has traditionally focused primarily on intercontinental invaders. However, our study uncovered the prevalence of intracontinental aliens. In Europe, 64.5% of the aliens have intracontinental origins, and, in Northern and Southern America, they make up nearly half of all alien species. This indicates that intracontinental aliens are, at least, as common as the intercontinental ones, indicating that intracontinental aliens require more research attention. A previous study, published in 2008, estimated a proportion of 7.5% intracontinental plants in North America (9). The apparent discrepancy with our finding may arise from the fact that the previous study mainly focused on invasive species (i.e., a subset of alien species causing impacts and being particularly widespread) and that many intracontinental aliens occur at lower abundances and have smaller alien ranges than intercontinental aliens (12). Furthermore, initially, many intracontinental aliens were not considered to be aliens as they are native in nearby regions. The only continent with a relatively low proportion of intracontinental aliens is Australia with 15.6%. Possibly, this reflects that the long biogeographical isolation of Australia makes its native flora unique (27) and vulnerable to invaders from other continents and that the wide variety of climates makes it particularly difficult for native species to naturalize to other regions within Australia.

The relationship between latitude and number of intracontinental aliens showed a different pattern between the two hemispheres. In the Northern Hemisphere, the number of intracontinental aliens peaked at mid-latitudes (around 40°). This is in line with the global latitudinal gradient of all naturalized aliens (fig. S3) (28). It likely reflects the strong biotic resistance in low-latitude regions (29), the high propagule pressure (30), and frequent human disturbance (31, 32) that aid naturalization in mid-latitude region and the stressful abiotic environments in high-latitude regions. In the Southern Hemisphere, the number of intracontinental aliens did not strongly change with latitude. For Australia, invasion patterns are probably influenced by the vast central deserts, which impede the naturalization of aliens there. For South America, the lack of latitudinal pattern may partly result from sampling biases as lists of native and naturalized species for this continent are less complete than those of the other three focal continents (26). In addition, human disturbance is still relatively low and recent compared to Europe and parts of North America and does not show a latitudinal pattern as strong as in the Northern Hemisphere (33). However, this also suggests that, with increasing development, South America is likely to host increasing numbers of aliens (34, 35), either inter- or intracontinental ones.

As the number of intracontinental aliens and the total number of aliens showed similar latitudinal patterns in the Northern

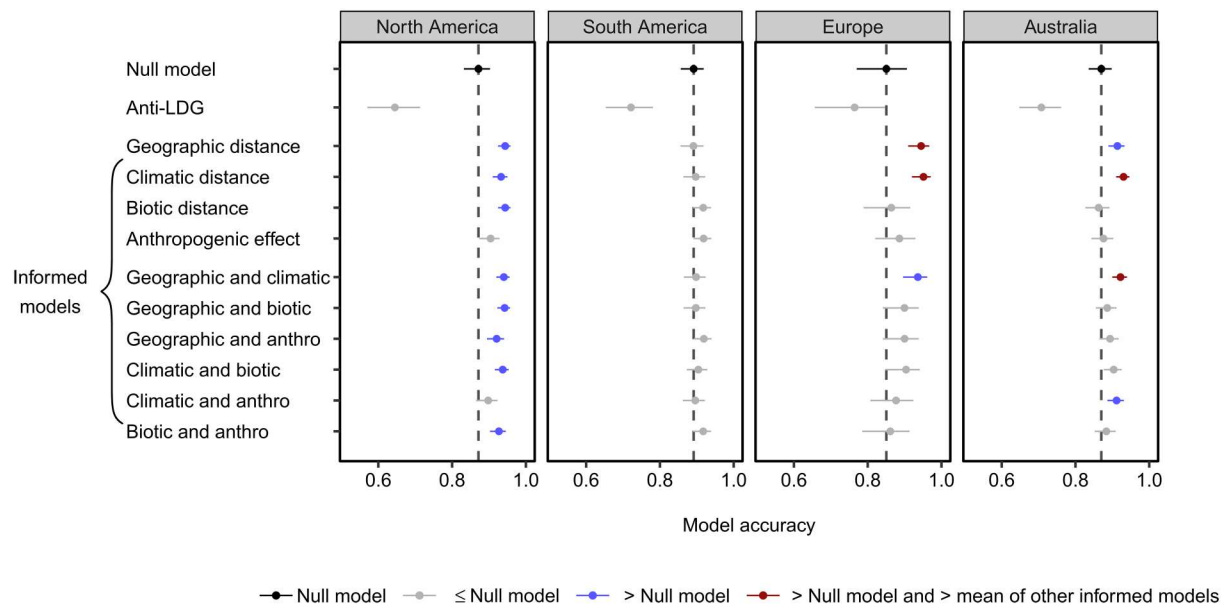


Fig. 4. Accuracies of models used to predict latitudinal shifts of intracontinental alien plants. The null model assumed that the intracontinental aliens in a recipient region were randomly drawn (naturalized) from the other regions. The anti-LDG model counteracts the LDG in native species (e.g., low and high latitudes contribute equally to species naturalization despite their difference in native species diversity; see Methods). Models informed by a single predictor assumed that the probability of a species naturalizing to a recipient region increased with the anthropogenic factor (GDP per capita) of the donor region or decreased with geographic, climatic or biotic distance between its native region(s) and the recipient region. Models informed by multiple predictors assumed that the probability of a species naturalizing to a recipient region was jointly determined by two or all of the three predictors (see Methods). Gray indicates models that did not outperform the null model (vertical dashed line), blue indicates models that outperformed the null model, and red indicates models that outperformed both the null model and the average of all other informed models. Error bars represent 95% CIs. South American regions that are located north of the equator were not included in the analysis.

Hemisphere, it is expected that the proportion of intracontinental aliens to all aliens did not strongly change with latitude. However, in Europe, the proportion rapidly increased with latitude. This is likely because human-mediated translocations, bringing numerous species from low to high latitudes, have allowed species to overcome the geographic barrier posed by longitudinally oriented mountain ranges such as the Alps and the relative geographic isolation of Scandinavia (36). In the Southern Hemisphere, the proportion of intracontinental aliens decreased with latitude. One possible explanation could be that intracontinental aliens are more likely to overcome the strong biotic resistance in low-latitude regions (i.e., tropics) than the intercontinental ones due to preadaptation. In addition, low- and mid-latitude regions in Australia host fewer native species (fig. S2) and thus can provide fewer intracontinental aliens to high-latitude regions.

Overall, intracontinental aliens have naturalized toward the poles. This is indicated by our finding that most regions have received more species from lower latitudes than from higher latitudes. This is also confirmed by analysis at the species level (Supplementary Method 1). Overall, intracontinental aliens naturalized toward the poles by 5.2 latitudinal degrees, which would correspond to distances more or less equal to the length of Poland or Ecuador. This also illustrates that intracontinental aliens naturalized toward colder regions (fig. S4) (37). A recent study found that birds mainly naturalized toward the equator (30). The contradiction between plants and birds may reveal the strong introduction bias toward the equator in birds, which promote their naturalization therein. However, despite the general trend of poleward naturalization, there is variation among species. While 49.8% of the species

expanded only their poleward boundaries, 9.2, 9.8, and 31.2% expanded only the equatorward boundaries, both boundaries, and neither of the boundaries, respectively (Supplementary Method 1).

Because lower latitudes usually host more native species than higher latitudes (known as the LDG), they can serve as major donor regions of intracontinental aliens and for nonassisted range expanders. Our null models of random naturalization already provided predictions that closely matched the observed latitudinal shifts, with accuracies of more than 85% for all four continents. Moreover, our anti-LDG models, which counteract the LDG in native species, were consistently outperformed by the null models. Furthermore, these models predicted less poleward naturalization than observed, except for Australia, where the LDG relationship is reversed. Together, our results suggest that the observed poleward naturalization of the intracontinental aliens largely resulted from the higher native species diversity at low than at high latitudes (38). In other words, in most continents, there is a larger pool of species that could naturalize toward higher latitudes than in the opposite direction.

The null models for each continent had already high predictive accuracies, particularly for South America, indicating random naturalization. In addition, it predicted more poleward naturalization than observed, suggesting that there might be more poleward naturalization with the continued introduction of alien species by humans. The inclusion of deterministic processes reduced the deviation between predicted and observed latitudinal shifts for Australia, Europe, and North America (Fig. 4 and fig. S5). For these three continents, latitudinal shifts of intracontinental aliens were consistently better predicted by models informed by climatic distance

and/or geographic distance. This indicates that climatic suitability and geographic distance have constrained naturalization. Although human introduction has greatly overcome dispersal barriers, intracontinental aliens are still more likely to succeed in regions that are geographically close to their native regions, most likely due to higher colonization and propagule pressures from the nearby regions and increased trade and associated dispersal between close regions (39). The strong predictive power of models informed by climatic distance indicates that intracontinental aliens mainly naturalize to regions that have climates similar to those in their native regions and thus that they have largely conserved their climatic niches. Studies on niche conservatism between native and alien distributions have shown mixed results (20, 21, 40), but cases of niche shifts or expansion have often been attributed to release from biotic interactions (40, 41). However, because intracontinental aliens have been found to be less released from biotic interactions than intercontinental ones (42), we hypothesize that climatic niche conservatism might be more prevalent in intracontinental aliens than in intercontinental aliens.

Unexpectedly, contrary to previous studies that consistently identified anthropogenic factors as the major determinant of naturalization success, we did not find such a relationship. One possible explanation is that variation in anthropogenic factors within continents is smaller than that across continents, making it challenging to detect their effect. Furthermore, our study only used one characteristic of the donor regions (GDP per capita) as a representative of the anthropogenic factors. This proxy may not fully capture the complex and multifaceted anthropogenic effects on species distribution (43). Bilateral relationships between recipient and donor regions (e.g., bilateral trade) (1) and/or direct measurements of propagule pressure (30) may provide more insights. However, we are not aware of these data at the scale and resolution of our study. Future studies are encouraged to test this hypothesis when these data become available.

Although we focused on species that have been introduced by humans, our findings are consistent with previous reports, across different taxonomic groups, of recent poleward range expansion of native species (43–46). This consistent pattern may arise from different mechanisms. The unassisted poleward expansion of natives is frequently attributed to their movement by natural dispersal in response to climate warming. Previous studies estimated that the mean velocity of poleward latitudinal expansion fell between 1 and 2 km year⁻¹ (43, 44). However, our research reveals a notable difference in the latitudinal shift of intracontinental aliens. These species naturalized toward the poles by a median of 572 km (5.2 latitudinal degree), which is much larger than the expected expansion due to climate warming alone (<100 km). This difference indicates that the current latitudinal shift of intracontinental aliens largely resulted from human assistance, as humans have introduced these species to suitable regions that are not easily reached through natural dispersal alone. Furthermore, the lesson learned from native range expanders suggests that climate change has the potential to accelerate the poleward naturalization by creating more climatically suitable regions in high latitudes, which deserves investigation in the future.

The last five centuries have seen rapid increases in anthropogenic translocations of species between continents (1). Our study revealed that the number of intracontinental alien plants is remarkably high, sometimes (e.g., in Europe) even surpassing the

number of intercontinental aliens. This finding might partly reflect that many early introduction for cultivation came from nearby regions within the same continent (47, 48), allowing these species more time to naturalize (47). The particularly high number of intracontinental aliens in Europe might be due to the long history of extensive land use and trade in this continent (49). We further revealed predominant poleward naturalization of intracontinental aliens, primarily due to larger native species pools at lower than at higher latitudes. Moreover, the latitudinal shifts of intracontinental aliens were even better predicted when we considered climatic suitability and geographic distance between their donor and recipient regions. Consequently, with continuing climate change, we will see increasing opportunities for aliens to establish in high latitudes as these regions become suitable for greater numbers of species, some of which will harm the economy and native biodiversity of the recipient regions.

METHODS

Data compilation and all analyses were conducted with R (version 4.2.0) (50).

Data compilation

We extracted regional lists of naturalized alien plant species from the Global Naturalized Alien Flora (GloNAF) database (26) and regional lists of native plant species from the Global Inventory of Floras and Traits (GIFT) database (25). GloNAF contains lists of naturalized [sensu Richardson *et al.* (51)] vascular plant taxa for 861 regions (countries or subnational administrative units), covering >80% of the terrestrial ice-free surface globally. GIFT contains lists of floras (predominantly native vascular plant taxa) for over 3000 regions, covering nearly 100% of the terrestrial ice-free surface globally. For the United States and Canada, we directly extracted the regional lists of naturalized alien and native species from the Biota of North America Program (52), whose last update was not included yet in GloNAF and GIFT when we started the analyses.

To ensure data quality, we filtered the dataset following Yang *et al.* (53). Briefly, we focused on flowering plants (angiosperms) because their species lists are more complete than those of other plant groups. We excluded lists that in GloNAF were classified as most likely very incomplete (26). We excluded hybrid taxa from the lists because their alien status and native origins are less clear. We only included aliens that are naturalized (i.e., were intentionally or nonintentionally introduced by humans and have established self-sustaining populations) according to the original data sources used in GloNAF. Unlike Yang *et al.* (53), we excluded islands because we focused on intracontinental aliens in contiguous regions within each focal continent. Because of the relatively low data coverage, we excluded regions of Asia (~26.4% coverage) and Africa (~25.2% coverage).

To merge the different datasets, we first selected regions that matched perfectly between GloNAF and GIFT. Second, to reduce variation in region size and to match GloNAF regions that are nested within GIFT regions and vice versa, we merged some small regions into larger regions using the *sf* package (version 1.0.7) (54). Third, to delineate the native ranges of the species within each continent as accurately as possible, we also included regions that have lists of native species but no lists of aliens. Fourth, we harmonized species names according to The Plant list (www.theplantlist.org/)

using the taxonstand package (version 2.4) (55). We only kept species with accepted names and used the binomial species names (i.e., intraspecific taxa were assigned to the binomial name). Last, for species with conflicting status (i.e., native to a region according to GIFT but naturalized to the same region according to GloNAF), we cross-checked their status with Plants of the World Online (56). We categorized a naturalized alien species as an intracontinental alien in a region when it is native to at least one other region within the same continent. Our final dataset included 264 regions that have lists of native species, 243 of which also have lists of naturalized species (fig. S6). The areas of the regions range from 166 to 2,074,433 km², with a median of 109,973 km². The dataset totals 660,466 native species-by-region records (127,398 species, ~41.8% of all flowering plants in the Plant List) and 92,320 naturalized species-by-region records (7950 species, ~2.6% of all flowering plants over the globe), 28,013 of which are naturalized intracontinental aliens (4510 species, ~1.5% of all flowering plants).

Numbers and proportions of intracontinental alien plants in regions at different latitudes

To test how the absolute number of intracontinental aliens and their proportion relative to all naturalized aliens change with latitude, we used GAMMs, which allow fitting nonlinear relationships, with the mgcv package (version 1.8.40) (57). The models included latitude, with cubic B-spline bases, as the fixed effect and continents as the random effect to account for the nonindependence of regions within continents. As the regions differ in size, we calculated natural log-transformed area-corrected numbers of intracontinental aliens following Fridley *et al.* (58). Briefly, we assessed the species-area relationship (in log-log space) for each continent, and we then used the median area of all regions to calculate the corrected species richness (on a log scale) for each region. Note that we used the median area to calculate a representative species richness across regions, although the choice of area size will not affect the test of significance of the latitude effect. To improve the normal distribution of the residuals, we logit-transformed the proportion of intracontinental aliens. The significance of fixed effects was assessed with *F* tests using analysis of variance (ANOVA).

Quantifying latitudinal shifts of intracontinental alien plants

We quantified the observed latitudinal shifts of intracontinental aliens as latitudinal changes from their native donor region(s) to the non-native recipient region (i.e., the region where they are now naturalized). Specifically, for each intracontinental alien per recipient region, we first calculated the native latitude of the species as the centroid latitude of its native region. For species with multiple native regions, we calculated the representative native latitude as the median latitude of all their native regions. We used absolute values of latitude, so that a high value indicates that the species is native to regions that are distant to the equator, irrespective of whether this is in the Southern or Northern Hemisphere. Then, for each recipient region, we calculated the overall native latitude of all intracontinental aliens in the recipient region as the median native latitude. Last, for each recipient region, we calculated observed latitudinal shift as the difference between the latitude of the recipient region and the median native latitude of the intracontinental aliens in the recipient region. A positive value of latitudinal shift indicates that the recipient region mostly received intracontinental aliens from lower

latitudes (i.e., that intracontinental aliens naturalized toward high latitudes), and a negative value indicates the opposite. Because South America has 12 regions in the Northern Hemisphere, using absolute latitude could bias the estimation of the latitudinal shift between donor and recipient regions. Consequently, we removed these regions from the analyses. To assess the overall latitudinal shifts of intracontinental aliens across the four continents and for each continent separately, we calculated bias-corrected 95% CIs of the median with 1000 bootstrap replicates.

Modeling latitudinal shifts of intracontinental alien plants

To identify determinants underlying latitudinal shifts of intracontinental alien plants, we ran different models to predict latitudinal shifts of intracontinental alien plants and assess their predictive accuracy. We started with a null model of random naturalization, in which, for each recipient region, species were randomly drawn (i.e., as naturalized species) from the native species in the other regions within the same continent. Mathematically, this means that the probability of a species being drawn (P_{drawn}) was constant. This means that it is more likely that species are drawn from species-rich regions, such as many low-latitude regions, and this model thus accounts for the LDG in native species (fig. S2). This model also accounts for the geographic constraint that the region with the highest latitude can only receive species from lower latitudes and that the region with the lowest latitude can only receive species from higher latitudes.

To explicitly test the effect of the LDG in native species on latitudinal shift, we ran a model that counteracted the LDG (hereafter anti-LDG model). Specifically, the model assumed that the probability of a species being drawn (P_{drawn}) is proportional to the inverse of the native species diversity at its latitude. Consequently, regions differing in native species diversity (e.g., equator versus pole) will contribute equally to species naturalization in the recipient region. To do this, we divided each continent into latitudinal bands of 1° (the results were qualitatively the same if we used bands of 0.5° or 2°). For each "latitudinal band," we determined the richness of native species, according to their native latitudinal ranges.

Subsequently, we ran informed models that assumed that the probability of a species being drawn (as a naturalized species) to a recipient region was determined by one of the following four factors: anthropogenic effect of the donor region (i.e., native region of a species), geographic distance, climatic distance, or biotic distance (see calculation below) between the recipient and donor regions. The anthropogenic effect-informed model assumed that P_{drawn} is proportional to the GDP per capita of the donor region. The geographic distance-informed model assumed that P_{drawn} is proportional to the inverse of the geographic distance between the recipient and donor regions. In other words, P_{drawn} decreased with geographic distance. Likewise, the climatic distance-informed model and the biotic distance-informed model assumed that P_{drawn} is proportional to the inverse of climatic distance or to [1 - biotic distance] of the native floras of the recipient region and that of the donor region. In cases of multiple donor (native) regions of a species, we used the maximum of GDP per capita and the minimum geographic, climatic, and biotic distances. This indicates that, for example, a species was likely to be drawn if the recipient region is close to its climatic niche margin (59). Alternatively, one can use the median of GDP per capita and the medians of the

geographic, climatic, and biotic distances. However, this method gave slightly less accurate prediction than the former (average accuracy of all models of using median values versus that of the former: 86.2% versus 86.8%).

In addition, we ran informed models that assumed that P_{drawn} was jointly determined by two of the four factors. Specifically, the models assumed that P_{drawn} is proportional to the geometric mean of the factors of interest (e.g., the geometric mean of the inverse of geographic distance and the inverse of climatic distance). As an alternative approach of combining multiple factors, we assigned each factor a certain weight and calculated the sum. However, this method requires additional parameter estimation and rarely outperformed the geometric mean method (Supplementary Method 2), indicating that the latter is robust.

A standard approach for calculating the expectations of these models is to draw for each recipient regions n species, where n is the number of intracontinental aliens, and to repeat this many times (e.g., 10,000 times) and to calculate the median of all replicates according to the "Quantifying latitudinal shifts of intracontinental alien plants" section. In Supplementary Method 3, we derived a theoretical expectation for these models and showed that the expectation is insensitive to the number of intracontinental aliens in the recipient regions.

We used GDP per capita as a proxy of anthropogenic effects. We extracted information on GDP per capita for the years 1990–2015 from Kummu *et al.* (60) for each region at a resolution of 5 arc min. As a region can contain multiple grid cells, we used the median value. We calculated geographic distance between regions as the distance between their geographic centroids using the *sf* package (version 1.0.7) (54). We also calculated the distance between the geographic borders. However, because the two methods showed a strong positive correlation ($n = 216,153$, $r = 0.996$, $P < 0.001$), we only used the former in our analysis.

We calculated climatic distance between regions based on their positions in multidimensional climate space. To do so, we extracted all 19 bioclimatic variables from the WorldClim (61) database for each region at a resolution of 2.5 arc min (i.e., each region consists of one or multiple grid cells). To reduce skewness of the data distribution, we square-root-transformed temperature seasonality (bio4), annual precipitation (bio12), precipitation of the wettest month (bio13), precipitation of the driest month (bio14), precipitation seasonality (bio15), precipitation of the wettest quarter (bio16), precipitation of the driest quarter (bio17), precipitation of the warmest quarter (bio18), and precipitation of the coldest quarter (bio19). As some of these bioclimatic variables are highly correlated, we first conducted a principal components analysis on them and used the first two principal component (PC) axes, which are orthogonal to each other and together explained 79.6% of the total variance, as new climatic descriptors (fig. S7). As a region can contain multiple grid cells, we used the median value of each PC as the representative PC score for each region. We calculated the climatic distance between regions as the Euclidean distance of the two PCs.

We calculated biotic distance between regions as the Simpson dissimilarity index (Eq. 1) (62), which is largely insensitive to species richness (63) (although using indexes that are sensitive to species richness, such as Sørensen dissimilarity, did not qualitatively

change the results)

$$\text{Dissim} = \frac{\min(b, c)}{a + \min(b, c)} \quad (1)$$

Here, a is the number of native species shared between both regions, b is the number of native species that occur in the first region but not in the second, and c is the number of native species that occur in the second region but not in the first. The Simpson dissimilarity index ranges from 0 to 1, with a high value indicating a high distance between regions. Geographic, climatic, and biotic distances were strongly correlated with each other for regions in North America and moderately correlated with each other for regions in the other three continents (fig. S8).

Assessing model predictive accuracy and identifying determinants underlying latitudinal shift

For a given recipient region (region i), we calculated the predictive accuracy (acc_i) as the deviation between the observed ($\text{shift}_{\text{obs}_i}$) and predicted latitudinal shifts ($\text{shift}_{\text{pred}_i}$), normalized to the largest possible latitudinal shifts of intracontinental aliens to the recipient region (Eq. 2)

$$\text{acc}_i = 1 - \frac{|\text{shift}_{\text{obs}_i} - \text{shift}_{\text{pred}_i}|}{\max\{|\text{margin}_{\text{south}} - \text{recipient}_i|, |\text{margin}_{\text{north}} - \text{recipient}_i|\}} \quad (2)$$

Here $\text{margin}_{\text{south}}$ and $\text{margin}_{\text{north}}$ are the latitudes of the most southern and the most northern regions of the focal continent (i.e., the continental margins), respectively, and recipient_i is the latitude of the recipient region. A high value of acc_i indicates a high predictive accuracy. For example, $\text{acc}_i = 1$ indicates that observed and predicted latitudinal shifts perfectly match for region i .

To assess model predictive accuracy and thus the potential determinants that best explain the latitudinal shifts of intracontinental aliens in each of the four continents, we conducted linear mixed-effect models (LMMs) for each continent with the *nlme* package (version 3.1.157) (64). The LMMs included predictive accuracy as the response variable, type of modeling approach (i.e., null model, anti-LDG model, and the informed models) as the fixed effect, and identity of region as the random effect (i.e., random intercept). Because regions with more intracontinental aliens have larger sample sizes, we weighted the data according to the log-transformed richness of intracontinental aliens. To improve the normal distribution of the residuals, we logit-transformed the predictive accuracy. We used multiple comparisons, with the *multcomp* package (65), to test (i) whether the anti-LDG model had lower predictive accuracy than the null model, (ii) whether the informed models had higher predictive accuracies than the null model, and (iii) which informed model(s) had higher predictive accuracies than the average of the other informed models. Significances of fixed effects were assessed with Z tests, corrected with the Benjamini-Hochberg (66) procedure to control for type I errors in multiple comparisons.

Supplementary Materials

This PDF file includes:

Figs. S1 to S13

Tables S1 and S2

Supplementary Methods

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The poleward naturalization of intracontinental alien plants

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