

Alien plants in the Anthropocene: exchange and accumulation of species around the world

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All around the globe, humans have greatly altered the abiotic and biotic environment with ever increasing speed. One defining feature of the Anthropocene^{1,2} is the erosion of biogeographic barriers by human-mediated dispersal of species into new regions, where they can naturalize and cause ecological, economic and social damage³. To date, no comprehensive analyses of global alien species accumulation and exchange between continents have been performed, primarily because of a lack of data. By using a unique global database on naturalized alien plant species occurrences in 481 mainland and 362 island regions, we bridge this knowledge gap. In total, 13,168 plant species, corresponding to 3.9% of the extant global vascular flora, or approximately the size of the native European flora, have become naturalized somewhere on the globe as a result of human activity. North America has accumulated the largest number of naturalized species, whereas the Pacific Islands show the fastest increase in species numbers with respect to land area. Continents in the Northern Hemisphere have been the major donors of naturalized alien species to all other continents. Our results quantify for the first time the extent of plant naturalizations worldwide, and illustrate the urgent need for globally integrated efforts to control, manage, and understand the spread of alien species.

The magnitude of impacts caused by alien species on native biota and human societies is increasing rapidly³. However, our knowledge of the global spread and distribution of naturalized species (i.e. alien species that form self-sustaining populations in new regions^{4,5}) is still very limited. Nevertheless, there are many presumptions about alien species regarding their distributions and pattern of spread. For example, it has frequently been suggested that Old World species have spread more widely outside their native ranges than New World species, owing to human colonization history or intrinsic evolutionary superiority^{6,7}, and that islands have more alien species than mainland areas, among others because of unfilled niche

space on islands^{7,8} or, as shown for birds, a higher introduction effort⁹. While these hypotheses have been tested for some parts of the world^{9,10}, global tests are still lacking.

Scientific and societal concerns about alien species have led to improved documentation of their distributions, and inventories have become available for many regions¹¹. Many of these inventories are still incomplete, especially for megadiverse taxonomic groups difficult to survey, such as invertebrates and microorganisms, and for less well-surveyed regions. However, vascular plants are well-documented because of long histories of exploration. Recently, there have been several major efforts to combine inventories of alien species for large geographic regions (e.g. DAISIE for Europe¹²), and for those considered to be the most problematic invaders globally¹³. However, a global database of the distribution of all naturalized alien plant species had not yet been built. Such data are essential for understanding global naturalization patterns and their underlying processes, reporting biodiversity status in terms of essential biodiversity variables¹⁴, and informing environmental managers across political borders *via* early warning systems.

Here, we present an analysis of naturalized vascular plant species in 843 non-overlapping regions (countries, federal states, islands) covering ~83% of the Earth's land surface (Fig. 1). We used a novel database, GloNAF (Global Naturalized Alien Flora), in combination with data on the origins of the naturalized species and estimates of the numbers of native species per continent, to assess (i) which continents have accumulated the largest naturalized floras, and (ii) which have been the major donors of naturalized alien plant species to other parts of the world.

We found that at least 13,168 vascular plant species have become naturalized in at least one of the 843 regions (including 362 islands) (Fig. 1). As there were no data available for c. 17% of the Earth's land area, particularly in temperate Asia (Fig. 1), and some of the

regional inventories used may not be fully comprehensive, the actual number is likely to be even higher. This means that at least 3.9% of all currently known vascular plant species on Earth ($n = 337,137$ [15]) have become naturalized outside their natural ranges as a result of human activity. With continuing globalization and increasing international traffic and trade, it is very likely that more species will be introduced outside their natural ranges and naturalize.

To assess which continents have accumulated the highest number of naturalized species, we assigned each of the GloNAF regions to the nine major biogeographically defined areas recognized by the Biodiversity Information Standards (TDWG¹⁶; Fig. 2a). Since these TDWG continents differ significantly in size, we created naturalized-species accumulation curves to allow comparisons of the number of naturalized plants per continent for equal areas to be made¹⁷. When ignoring differences in total area, North America has the highest cumulative number of naturalized species ($n=5,958$), followed by Europe ($n=4,140$, Fig. 2b). Although the rich naturalized floras of these continents could partly reflect a higher sampling intensity in these continents, it is likely that they also reflect a higher introduction effort. Both continents have dominated international trade for centuries, and many plants have been intentionally introduced from other continents for agricultural and horticultural purposes^{18,19}.

Although North America has a longer history of European colonization than Australasia, it received only slightly more naturalized species from outside the continent (3,513) than the latter (3,371; Fig. 2c). However, Australasia has even more such extra-continental species than North America when taking into account area differences (Fig. 2c). One possible explanation is that Australia's long biogeographical isolation and drying climate have resulted in a native flora that is phylogenetically distinct²⁰, but not well-adapted to exploit the novel habitats created by European settlers. These new habitats have instead been occupied by many incoming alien plant species.

When only extra-continental arrivals are considered, Europe drops to the 5th position, just behind Africa (Fig. 2c). Thus, while many plants from other continents have been introduced into Europe^{19,21}, surprisingly few of them have naturalized. One explanation may be that plants that spread through Europe with agriculture several thousand years ago (so-called archaeophytes) and European species that naturalized within the continent more recently, have already occupied many of the vacant niches, preventing many extra-continental species from naturalizing. In addition, extra-continental species may be relatively maladapted to the human-dominated environments in Europe, compared to species already present there, which have a longer evolutionary history of growing in these environments⁶.

The Pacific Islands show the steepest increase in cumulative number of naturalized species with area (Fig. 2). Therefore, our data provide the first global test, illustrating that oceanic islands harbour more naturalized alien plants than similarly sized mainland regions, a phenomenon that is attributed to the available niche space not being saturated by native species^{8,22} or to a higher number of introductions. Given the high concentration of endemic species on most oceanic islands²³, the great richness of naturalized species on these islands constitutes a serious threat to global biodiversity.

TDWG continents with large tropical regions (Africa, South America and tropical Asia) have overall fewer naturalized alien species than the predominantly temperate continents (North America, Europe and Australasia). This is consistent with previous observations suggesting a higher resistance of tropical regions to alien-species establishment because of fewer available free ecological niches, faster recovery of vegetation following disturbance or a lower introduction rate^{7,24,25}. Temperate Asia, in contrast, showed a very low rate of naturalized species accumulation with area. Unlike other continents, most of temperate Asia has not been colonized by Europeans²⁶, and large parts of it have only recently opened up to inward movements of people and plants²⁷. With the recent rise of China as a major trade

partner, we might expect a rapid increase of naturalized species in temperate Asia in the coming decades.

To identify the major donor continents of naturalized alien plant species, we assigned each naturalized species to its native continent(s). Based on estimated numbers of native species per continent, one would expect the most species-rich TDWG continents (South America and tropical Asia) to be the main donors of naturalized plant species (Fig. 3a); but they are not. The observed flow of naturalized plant species clearly shows that temperate Asia and Europe are the major donors (Fig. 3b). While temperate Asia is ahead of Europe in absolute numbers, the observed number of species native to Europe and naturalized elsewhere is 288% higher than expected, but only 52% higher than expected for temperate Asia (Extended Data Fig. 1; Extended Data Table 1). Furthermore, North America is also overrepresented, with 57% more species donated than expected (Extended Data Fig. 1). In contrast, the TDWG continents that are largely in the Southern Hemisphere are all underrepresented as donors (Extended Data Fig. 1). These results are robust against potential over- or underestimates of the number of native species per continent (see Supporting Information for a sensitivity analysis). This suggests that the traditionally acknowledged Old World vs New World dichotomy in biological invasions^{6,7} needs to be replaced by a Northern vs Southern Hemisphere dichotomy with regard to the donor continents of naturalized alien plants globally. Darwin²⁸ suggested that Northern Hemisphere species, as a consequence of a more competitive evolutionary history, are intrinsically better competitors than Southern Hemisphere species, and that this could explain their naturalization success. To determine whether this is indeed the case requires further research. Nevertheless, the fact that the Southern Hemisphere is currently underrepresented as a donor, might also indicate that the southern continents still harbour many species that could potentially spread to northern continents when given the chance.

For six of the nine TDWG continents, the observed intra-continental flows were larger than expected (Fig. 3, Extended Data Fig.1). Because of the shorter distances, intra-continental propagule pressure can be assumed to have been larger, and because of environmental similarity subsequent naturalization chances are higher for intra-continental alien species²⁹. Notable exceptions with fewer than expected intra-continental naturalizations were South America and tropical Asia. We argue that because many species from these continents have restricted ranges – reflected in relatively high levels of regional endemism²³ – species from tropical Asia and South America are less likely to have been dispersed outside their native ranges.

The recently compiled GloNAF database has enabled the most comprehensive analysis to date of the global distributions of naturalized alien plant species, and provides the first robust estimates of the flows of naturalized plant species worldwide. We reveal striking differences within and among continents in the sizes of their naturalized alien floras, rates of accumulation of naturalized species with respect to area, and relative importance as exporters of naturalized species. Humans have strongly shaped the geographic composition and global distribution of alien plants among the World's continents, with the Northern Hemisphere being the major donor. The Pacific Islands and Australasia harbour the highest numbers of naturalized alien species, given their sizes and the extent of naturalization of species from other continents. The GloNAF database and the robust large-scale patterns we reveal here provide a vital foundation for testing fundamental hypotheses to better understand plant naturalization. For example, when combined with native plant inventories and phylogenetic data, the database will allow quantification of the degree of global floristic homogenization and tests to determine whether naturalized species are more closely or more distantly related to native species²⁸. In addition, the global baseline data of plant naturalizations provided here may contribute an essential biodiversity variable needed to monitor changes in global

biodiversity¹⁴, and can inform evidence-based alien species management.

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Figure 1 | Naturalized vascular plant species in the 843 regions covered by the GloNAF database. The heat-map colours correspond to the number of naturalized species in each of the regions (including 362 island regions). Areas permanently covered by ice sheets are indicated in hatched cyan blue. Grey areas indicate regions lacking naturalized plant data. To allow comparisons between the sizes of the GloNAF regions, we used a Mollweide equal-area projection. However, to increase the visibility of small islands and island groups on the map, they are represented by circles.

Figure 2 | Naturalized species-accumulation curves for the major biogeographic areas. **a**, Map of the nine TDWG continents. Hatched areas indicate major permanent ice sheets. **b**, Naturalized species-accumulation curves (1,000 random draws) for each of the nine continents. **c**, Same as **b** but here naturalized species are restricted to extra-continental aliens only. The colours in **b** and **c** correspond to the colours of the continents in **a**. Vertical and horizontal dashed lines mark the total area and the total number of naturalized plants, respectively. To increase visibility, thicker lines were used for Pacific Islands and Antarctica.

Figure 3 | Flows of naturalized alien plant species among the TDWG continents. **a**, Expected flows (medians of 999 random draws) of naturalized species based on estimated numbers of native species (in brackets). **b**, Observed flows of naturalized species. The continents are ordered according to decreasing importance as sources. Only the 50% most important flows are shown. Ant.: Antarctica (n = 293 native species), C: only known from cultivation or novel hybrids (n = 97 species). Each tick along the outer circle corresponds to 1,000 species. Left parts of inner bars along the circle represent flows of imported species, right parts exported species.

METHODS

Data compilation. The GloNAF database includes inventories of naturalized alien plant species (also including infraspecific taxa and hybrid taxa) for 843 regions worldwide. The data sources that we used (see Supplementary Data) include naturalized alien plant compendia, national and subnational lists of naturalized alien plant species published in scientific journals, as books or on the internet, as well as books and online compendia of national or subnational floras with information on which species occur in the wild but are not native³⁰. Our database also includes unpublished inventories of naturalized alien species that were specifically compiled for the GloNAF database (e.g. for the provinces of China and the states of India). We consider those alien species that have established self-sustaining populations without direct human intervention to be naturalized following Richardson et al.⁴ and Pyšek et al.³¹. The GloNAF database will be fully publicly available after finalizing funded GloNAF projects (Deutsche Forschungsgemeinschaft DFG, Austrian Science Fund FWF), which are due in c. 3 years.

As certain regions of the world are more intensively researched than others, it is unavoidable that some of the regional inventories of naturalized alien species are more comprehensive than others. We aimed at including the most comprehensive and most recent regional inventories. Indeed, >95% of the data sources are from the last two decades (see Supplementary Data). Moreover, since some of the original source lists included alien species that are cultivated only or have non-persistent populations in the wild, we excluded those species whenever such information was provided, or contacted experts of the regional floras to remove species of doubtful naturalization status. Furthermore, for European countries that differentiated between archaeophytes (alien species that came before the year 1492) and neophytes (species that came after the year 1492), we kept only the latter, because the alien status of some species classified as archaeophytes is disputed; moreover, this classification is

not available for other regions of the world, and thus would prevent us from achieving a balanced/standardized assessment of naturalized alien species numbers.

To standardize scientific names, each naturalized plant inventory was compared to The Plant List¹⁵, the most comprehensive working list of all plant species³². This taxonomic standardization was done with the help of the R³³ package *Taxonstand*³⁴. For each species, we kept the name accepted by The Plant List. Species that were not found in The Plant List, also not after accounting for spelling differences, were kept in the database using the names as used in the source data. In total, the database includes 13,168 species of which 13,033 are recognized by The Plant List (12,498 as accepted and 535 as unresolved names). The remaining 135 species do not occur in The Plant List, and among those 11 are ornamental cultivars.

For each species in the database, we compiled data on which of the nine regions of the TDWG continental scheme (further referred to as TDWG continents¹⁶) the species is native to, or whether they are known only from cultivation or resulted from hybridization between two alien species or an alien and a native species. Most of the native-range data were extracted from the World Checklist of Selected Plant Families³⁵ (WCSP), and supplemented with data from the Germplasm Resources Information Network³⁶ (GRIN). For the c. 4,000 species that were not included in these two major data sources, we retrieved information on the native regions from printed floristic compendia, extensive internet searches and comparisons of their naturalized distributions to their overall distributions in the Global Biodiversity Information Facility³⁷ (GBIF). Native-continent information was found for 13,070 species, of which 219 are only known from cultivation and 51 are novel hybrids. Many (5,646) species were native to more than one continent. For the few (98) remaining species, we could not find any information on their native ranges.

Each of the 843 regions covered by GloNAF was assigned to one of the nine TDWG continents. We calculated the area of each region while considering only the ice-sheet free areas of each region, ranging from 0.03 to 2,486,952 km², with a median of 18,725 km².

Accumulation of naturalized species per continent. To determine which continent accumulated the highest number of naturalized species for a certain area, we constructed species-accumulation curves¹⁷ separately for each of the nine TDWG continents. Since choosing a starting region and the order of adding remaining regions to the species-accumulation curves would be arbitrary, we used a random order of regions, and repeated this procedure 1,000 times. Species-accumulation curves were calculated for all alien species and for extra-continental alien species separately. This analysis was done in the R package *vegan*³⁸.

Flows of naturalized alien species among continents. To test whether the observed flows of naturalized species from donor continents to recipient continents are larger or smaller than expected, we compared the observed flows to the ones based on random draws from the extant global flora. Since no data on the number of native species per TDWG continent exist, we first estimated these numbers by extrapolation of the known native origins of 130,641 accepted vascular plant species in the WCSP³⁵ to the total number of 337,137 accepted species in The Plant List¹⁵. Although the WCSP³⁵ includes quite a large proportion (38.8%) of all vascular plant species, it does not include all vascular plant families yet, and it might be geographically biased. However, Joppa et al.³⁹ showed that all 52 TDWG-level-2 regions, and thus the TDWG continents also, are well represented in the WCSP. Furthermore, our estimates did not deviate much from published estimates we found for some of the continents: Our estimate of 62,193 native species for Africa is close to the previously

estimated 40,000-60,000 for the African mainland⁴⁰, and the 64,500 species listed in the African Plants Database³⁰. Our estimate of 14,148 native species for Europe is slightly higher than the 12,517 native species listed in the Flora Europaea⁴¹. Our estimate of 30,054 native species for North America is higher than the 21,500 species listed in the Biota of North America Program⁴² (BONAP), but the latter does not include species of Mexico. Our estimate of 22,891 native species for Australasia is higher than the 19,324 reported for Australia by the Australian National Herbarium⁴³, but the latter does not cover all parts of Australasia (e.g. New Zealand). Therefore, while our estimates of the native species richness of each continent are higher than previous estimates, these differences seem to result mainly from additional regions included in TDWG continents and gaps in the other data sources. Thus our results appear to be realistic proxies for the true numbers of continental species richness.

To obtain the expected flows of species from donor to recipient continents, we first created a species pool with a size equal to the one of the extant global species pool ($n = 337,137$) in which the proportion of species native to each continent or combination of continents was based on the estimated native species richness of the continents. Then for each recipient continent, we drew separately a random sample of species from the extrapolated global species pool. The size of the random sample was equal to the number of naturalized alien species observed in the recipient continent. We then recorded the number of randomly drawn species native to each continent or belonging to the pool of species that are only known from cultivation or as novel hybrids. This random-draw procedure was repeated 999 times, and the medians are shown in Fig. 3a. We did this for each recipient continent separately to allow for the fact that a species can be naturalized in more than one continent. If the observed flow of species from a donor continent to a recipient continent was within the upper 2.5% of the random distribution, we considered the observed flow to be significantly

larger than expected by chance, and if the observed flow was within the lower 2.5% of this distribution, we considered the flow to be significantly lower than expected by chance. Since we might have over- or underestimated the native species richness for some continents, we also did a sensitivity analysis by decreasing and increasing the size of the native flora of each continent by 10% in turn (see Supplementary Information). R syntax for the random draws is available from the corresponding author on request. Flow plots were created using an R syntax adapted from Abel and Sander⁴⁴.

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Extended Data Figure 1 | Observed and expected numbers of naturalized species from each donor TDWG continent in each of the recipient TDWG continents. Histograms of the expected numbers are shown in black open bars, and are based on 999 random draws from the global flora. The observed numbers are shown as vertical lines; blue: significantly fewer observed naturalized species from the source continent than expected (in the lower 2.5 percentile), red: significantly more observed naturalized species than expected (in the upper 2.5 percentile), black: the observed number of naturalized species is within the central 95% range of the expected numbers.

Extended Data Table 1 | Results of sensitivity analysis for observed and expected numbers of naturalized species from each donor continent in each of the recipient continents. For each combination of two TDWG continents, the table gives the observed number (No.) of species that are native to the donor continent and have become naturalized in the recipient continent in bold. Below, each observed number is the median of the expected number based on 999 random draws from the global vascular flora. Below this median, the minimum and maximum median of the expected numbers found during the sensitivity analysis are given in italics. In addition, the table gives the proportion (P) of the 999 random draws for the expected values that were smaller than the observed value. The minimum and maximum proportions found during the sensitivity analysis are given in italics. Proportions >0.975 (the source is overrepresented in the recipient continent) are given in red and proportions <0.025 (the source is underrepresented) are given in blue.

Supplementary Information

Sensitivity analysis for testing whether the observed flows of species between TDWG continents are larger or smaller than expected

We tested whether the observed flows of species between continents are larger than, smaller than or equal to the expected flows of species based on random draws from the global vascular flora (337,137 accepted species in The Plant List; TPL 2015). The number of species from the global vascular flora that are native to each of the TDWG continents were estimated by extrapolation of the known native origins of 130,641 accepted vascular plant species in the world checklist of selected plant families (WCSP; 2014). Although the WCSP (2014) includes 38.8% of all vascular plant species, it does not include all vascular plant families, and it might be geographically biased.

To test how sensitive our analysis of flows is to such a potential geographic bias in the estimated number of native species per continent, we performed a sensitivity analysis. As the estimated number of native species in each continent might be either lower or higher than the estimate that we used, we repeated our analysis after reducing and after increasing the number of native species in a continent by 10%, while keeping the numbers of native species for the other continents constant. This resulted in 18 new series (a 10% decrease and a 10% increase for each of the nine TDWG continents) of 999 random draws to which we compared the observed flows. In Extended Data Table 1, we present for each flow from a donor to a recipient continent the minimum and maximum medians of the 18 series of 999 random draws, as well as the minimum and maximum proportions of each of the 999 draws that were smaller than the observed flow. The results of this sensitivity analysis indicate that our tests are robust against potential over- or underestimation of the numbers of native species in each

continent as there were only minimal changes in the proportions of random draws smaller or larger than the observed values.





