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Global trade will accelerate plant invasions in emerging economies under climate change

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Abstract

Trade plays a key role in the spread of alien species and has arguably contributed to the recent enormous acceleration of biological invasions, thus homogenizing biotas worldwide. Combining data on 60-year trends of bilateral trade, as well as on biodiversity and climate, we modeled the global spread of plant species among 147 countries. The model results were compared with a recently compiled unique global data set on numbers of naturalized alien vascular plant species representing the most comprehensive collection of naturalized plant distributions currently available. The model identifies major source regions, introduction routes, and hot spots of plant invasions that agree well with observed naturalized plant numbers. In contrast to common knowledge, we show that the 'imperialist dogma,' stating that Europe has been a net exporter of naturalized plants since colonial times, does not hold for the past 60 years, when more naturalized plants were being imported to than exported from Europe. Our results highlight that the current distribution of naturalized plants is best predicted by socioeconomic activities 20 years ago. We took advantage of the observed time lag and used trade developments until recent times to predict naturalized plant trajectories for the next two decades. This shows that particularly strong increases in naturalized plant numbers are expected in the next 20 years for emerging economies in megadiverse regions. The interaction with predicted future climate change will increase invasions in northern temperate countries and reduce them in tropical and (sub)tropical regions, yet not by enough to cancel out the trade-related increase.

Keywords: alien vascular plants, bioinvasion, climate warming, global spread, imperialist dogma, model, network of plant invasion

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Introduction

Numbers of alien species are rapidly increasing worldwide (Lambdon *et al.*, 2008; Hulme *et al.*, 2009; McGeoch *et al.*, 2010; Winter *et al.*, 2010), and so are the impacts they cause (McGeoch *et al.*, 2010; Vilà *et al.*, 2011; Pyšek *et al.*, 2012a; Simberloff *et al.*, 2013). Global trade plays a key role in the spread of alien species as many of them are introduced by means of trade and transport (Meyerson & Mooney, 2007; Hulme, 2009; Pyšek *et al.*, 2010; Essl *et al.*, 2012). The amount of exchanged commodities expanded more than 30-fold on average since 1950 but with distinct variations among countries as some economies grew more strongly and at different times than others (World Trade Organization, 2007). Both the quantitative and qualitative changes of global trade affect the spread of alien species (e.g., Dalmazzone, 2000; Vilà & Pujadas, 2001; Levine & D'Antonio, 2003; Westphal *et al.*, 2008). For example, the relative increase in trade volume of emerging economies should have intensified the spread of alien species from and to these countries. However, the true consequences of global trade on invasions have most likely not yet been observed due to substantial time lags between socioeconomic activity and the increase in the levels of biological invasions it brings about (Essl *et al.*, 2011).

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It has been argued that the interaction with other features of global change, in particular climate change, will foster further spread of alien plants (Settele *et al.*, 2014; but see Early & Sax, 2014). The predicted increases in temperature, for instance, are likely to allow species to expand their range to regions that were formerly too cold for survival (Walther *et al.*, 2009). In tropical regions, however, the influence of climate change on alien species is less clear as a further increase in temperature may also hamper the establishment of new alien species because most species are not adapted to such high temperatures (Thomas *et al.*, 2004). The interacting effects of globalization and climate change on biological invasions may be profound but comprehensive analyses are still lacking.

Here, we use a recently compiled unique global data set of numbers of naturalized alien vascular plant species (hereafter 'naturalized plants') per country, data on annual bilateral trade value between countries between 1948 and 2008, and a wide range of environmental country-specific variables to test which factors best predict the richness of regional alien floras. We adopted a model developed for marine invasions (Seebens *et al.*, 2013) to (i) analyze the role of the global trade network on the total number of naturalized plants in countries, (ii) identify whether and to what extent the richness of regional alien floras lags behind recent increases in trade, (iii) predict the extent of future distributions of naturalized plants, (iv) identify major source regions and introduction routes, and (v) analyze the interaction of trade-related drivers with climate change in accounting for future spread of alien plants. While the influences of trade and climate change on the spread of alien species have been analyzed elsewhere (Walther *et al.*, 2009; Pyšek *et al.*, 2010), this study is the first analyzing their combined effect on a global scale for a major taxonomic group. The established model enables us to disentangle the complex relationships between globalization, biological invasions, and climate change and to project trajectories of future plant invasions.

Materials and methods

The model applied in this study integrates different aspects from network theory and environmental niche modeling as its backbone represents the combination of the global trade network with environmental similarities of countries. We established 11 different model versions incorporating different potential predictors for alien plant invasion. Each model version was first trained (parameterized) using a data set of global flows of alien plant species and afterward tested using an independent, novel, and unique global data set of alien plant species numbers. The best-fitting model is presented below, while other model versions and their predictions are shown in the Supporting Information.

Modeling the role of trade, climate, and donor region biodiversity in alien plant invasion

The final best-fitting model requires the following input variables: Bilateral trade shares, environmental and geographic distance between countries, and the number of native plant species in the donor country.

Bilateral trade data. Data of bilateral trade between countries were taken from http://privatewww.essex.ac.uk/~ksg/exptradegdp.html (Gleditsch, 2002). This trade data set comprises the annual amount of trade value exchanged between countries from 1948 to 2000, given in millions of current year $US (Fig. S1). We selected only those countries for which we also had environmental data and the number of native vascular plant species. The numbers of reported countries and trading partners increase over time from 76 countries and 5700 country–country pairs in 1948 to 186 countries and 34 410 pairs in 2000 (Fig. S2). A second data set of bilateral trade obtained from the 'Correlates of War' (COW) project (Barbieri *et al.*, 2009) spans a longer time period (1870 to 2009), but the number of links and nodes is reduced compared to the data set provided by Gleditsch (see 'Sensitivity Analysis' in the Supporting Information for a detailed comparison of both data sets). The COW data were used to test the robustness of the results and to fill the gaps in the Gleditsch data set from 2001 to 2008.

Environmental and country data. Data of country-wise annual mean temperatures, annual mean precipitation, and altitude were compiled from the WorldClim database (www.worldclim.org, Hijmans *et al.*, 2005). WorldClim provides global maps of these measures at a resolution of 5 arc minutes (Fig. S3), and these were used to calculate the mean values for every country. The distance between countries was measured as the great circle distance between the centroids of all countries. The centroids were calculated from the world maps provided in the R package 'maptools' (Bivand & Lewin-Koh, 2013).

For the forecast of climatic changes, we selected the A1B scenario, that is a medium-range IPCC climate change scenario, which projects an average global temperature increase of 1.4 °C for 2020–2029 relative to 1960–1990 (Fig. S4, IPCC, 2007). The A1B scenario is based on a story line that assumes rapid economic growth, a human world population that peaks mid-century and declines thereafter, and rapid introduction of new and more efficient technologies. We used the model results derived from the widely used general circulation model ECHAM5 (Roeckner *et al.*, 2003). From a 2.5-arc-minute resolved data set, we calculated the predicted mean temperature and precipitation for all countries. The data are provided by the CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS, http://ccafs.cgiar.org).

Native vascular plant data. We assume that the number of potential new invaders should be higher for large species pools compared to smaller ones. This assumption is related to the hypothesis of Sax & Brown (2000) who suggested that colonists from large, species-rich regions possess superior quality as invaders due to the historical contingency of evolution. This can be expected because invaders native to such large species-rich regions sampled a wider range of environmental variation and encountered more interactions with other native species in their evolutionary history in the native range. Indeed, Kalusová *et al.* (2014) showed that the number of alien plant species increases with the size of the donor species pool. We therefore considered the numbers of native vascular plant species S per donor country i as a predictor variable in the model (Eq. 2). Data of native plant species numbers were compiled for 166 countries and taken from the recently assembled beta version of the GloNAF database (‘Global Naturalized Alien Flora,’ access date: November 15, 2013, Fig. S3). GloNAF is a continuing data collection comprising country-wise numbers of native and established alien vascular plant species. It is by far the most complete database on alien plant species distributions worldwide. GloNAF has been developed by a group of invasion ecologists that are part of the author team of this article.

Model. The model is adopted from a study on marine invasions (Seebens *et al.*, 2013) and slightly modified to capture the dynamics of alien plant invasions. In particular, the environmental conditions and the introduction vector considered in the model were adjusted. The model presented here calculates the probability that a vascular plant species native to country i and non-native to country j is introduced to j and establishes a population within a time period τ. The model accounts for the fact that invasion is a multistage process (Blackburn *et al.*, 2011): For a successful invasion, (i) the species must be non-native to the new country, (ii) it must be transported to that country, and (iii) it must be able to survive and reproduce in the new environment. An independent probability is assigned to each of the three stages.

The probability P_{ij}(Alien) describes the likelihood that species native in country i are non-native in country j

$$P_{ij}(\text{Alien}) = \left(1 + \frac{\gamma}{D_{ij}}\right)^{-\beta}. \tag{1}$$

This probability is estimated by the great circle distance D_{ij} between countries as according to general findings of other studies, we assume that biogeographical dissimilarity increases with geographic distance (Tuomisto *et al.*, 2003; Soininen & Hillebrand, 2007; Thieltges *et al.*, 2009). At short distances of several hundreds of kilometers, however, most plant species are shared by national floras due to climatic and habitat similarities and the predominant absence of strong dispersal barriers. Accordingly, the distribution of species is mainly determined by environmental filtering rather than dispersal limitation. Thus, most native plant species in adjacent countries do not qualify as potential alien species. Consequently, the increase in P(Alien) should be disproportionally low at short distances compared to large distances. As P(Alien) is a probability, it has to asymptotically approach one for large distances, which gives rise to a sigmoid shape of P(Alien). Here, $\beta > 0$ is a shape parameter and γ denotes the characteristic distance below which P_{ij}(Alien) changes at disproportionally low rate, that is, the inflection point of the sigmoid function. Ignoring P(Alien) in the model would drastically increase the invasion probability at short distances. P(Alien) is therefore a crucial component of the model controlling invasion probabilities at short distances.

The probability of introduction P_{ij}(Intro) defines the probability that a species is transferred from i to j by the transport of commodities. P_{ij}(Intro) depends on the cumulative amount of transported commodities G_{ij} measured in million \$US. We used cumulative trade values (i.e., the sum of all $G_{ijy} = \sum_{t=1948}^{y} G_{ijt}$ from 1948 to the year y under investigation with G_{ijt} being the trade value exchanged between i and j during year t) to account for the fact that species were introduced continuously during the last decades. The cumulative probability of introduction P_{ijy}(Intro) also increases with the number of native species S_i in the donor region as the number of potential new invaders should be higher from regions of high biodiversity. P_{ijy}(Intro) is modeled as the product of the complement of exponential functions

$$P_{ijy}(\text{Intro}) = \left(1 - e^{-\delta G_{ijy}}\right)\left(1 - e^{-\lambda S_i}\right) \tag{2}$$

with δ and λ being characteristic constants.

The probability of establishment P_{ij}(Estab) is a function of the environmental similarity between donor and recipient regions. The environmental similarity is modeled as the difference in annual mean temperature ΔT_{ij}, annual mean precipitation ΔP_{ij}, and mean altitude ΔA_{ij} between countries standardized by the standard deviations σ_T, σ_P, and σ_A, respectively. P_{ij}(Estab) is modeled by a Gaussian function,

$$P_{ij}(\text{Estab}) = \alpha\, e^{-\frac{0.5}{3}\left[\frac{\Delta T_{ij}}{\sigma_T} + \frac{\Delta P_{ij}}{\sigma_P} + \frac{\Delta A_{ij}}{\sigma_A}\right]}, \tag{3}$$

where α denotes the initial probability of invasion. For terrestrial plants, these environmental parameters have long been assumed to be the most important ones to characterize their ecological niches (Cain, 1944). All three parameters are only weakly correlated as the correlation coefficients for all parameter combinations were always smaller than $|0.33|$.

Our numerical simulations show that these three probabilities are only very weakly correlated (Fig. S5). Assuming statistical independence, the probability of invasion, P_{ij}(Inv), from country i to country j within a time period τ, is obtained by the product of the above probabilities. The invasion risk of a single country j can be calculated as the complement of the product of the probabilities of all failing invasion attempts into that country:

$$P_j(\text{Inv}) = 1 - \prod_i \left[1 - P_{ij}(\text{Alien}) P_{ijy}(\text{Intro}) P_{ij}(\text{Estab})\right]. \tag{4}$$

Testing model performance

We first parameterized the model (i.e., estimated the unknown parameters: y, α, β, γ, δ, λ, σ_T, $\sigma_{P,}$ and σ_P) using a training data set comprising the global flows of naturalized plants between regions. Once the best setting of parameter values was identified, the model performance was tested using an independent data set of naturalized plant numbers per country. In particular, we did the following.

To obtain the training data set, we gathered native and alien ranges of naturalized plants of 12 countries from all inhabited continents of the world from the literature (Table 1). These data were used to construct a network of reported plant invasions, which gives the numbers of alien plants transferred from a region of origin to a country, where the species naturalized. This network of reported plant invasions allows a direct comparison of the reported flows of naturalized plants with those predicted by the model and thus was used as the training data set to parameterize the model.

The native regions in the selected case studies are usually defined at coarse geographical resolutions, for example, North America, Mediterranean, or Middle East, which we adopted. That is, we aggregated the model predictions in the same way as carried out in the respective case study to compare reported and predicted naturalized plant species numbers. We explicitly excluded countries with a large number of plant invasions during colonial times such as the USA, Canada, Australia, and New Zealand as our approach cannot capture pre-1900 introductions due to missing trade data. We also excluded countries that split after World War II into two or more successor states (e.g., Czech Republic, Slovakia, and successor states of the former Soviet Union), as historical trade data of the united countries do not qualify as predictors for recent naturalized plants accumulation in the successor countries. Altogether, data on 9,138 records of naturalized plants for 113 combinations of a native region and an invaded country were obtained (see 'Model parameterization' in Supporting Information).

For comparison of observed and predicted species numbers, we calculated the expected number of establishments from country i to country j during the time period τ as $E_{ij}(\mathrm{Inv}) = -\log\ [1 - P_{ij}(\mathrm{Inv})]\ \tau$, with τ set to 1 year. The expected number of naturalized plants, $E_{ij}(\mathrm{Inv})$, was compared to the reported number of naturalized plants, $N_{ij}(\mathrm{Inv})$, provided by the training data set. The deviation between $E_{ij}(\mathrm{Inv})$ and $N_{ij}(\mathrm{Inv})$ data was calculated by the root-mean-squared error, $\mathrm{RMSE} = \sqrt{\sum \left[E_{ij}(\mathrm{Inv}) - N_{ij}(\mathrm{Inv})\right]^2 / n}$, with $n = 113$ being the number of observed combinations of native and alien ranges in the 12 case studies of the training data set. A low RMSE indicates small deviations between model predictions and field data. The optimal parameter values were obtained by minimizing the RMSE with a nonlinear optimization algorithm (simulated annealing, Kirkpatrick *et al.*, 1983). In our study, simulated annealing used more than 16 000 optimization steps, it was started three times with a different random initialization of parameters for each year y under investigation, and the best fit was selected.

Once the best-fitting set of parameter values was identified, the model predictions were tested using an independent, novel, and unique data set of naturalized plant numbers per country taken from the GloNAF database (see above and Fig. 1a). At the GloNAF access date, information on naturalized plants was available for 119 countries. In collecting the data for

Table 1 List of case studies providing information about native ranges of alien plants for various countries worldwide. From these data, a network of reported plant invasions was constructed, which was used as a training data set to parameterize the model. In total, 9138 records of naturalized plants for 113 combinations of a native region defined on a coarse geographical scale such as North America or Middle East and an invaded country were obtained

Country	Data source
Argentina	Nicol Fuentes, unpublished data.
Austria	Essl F, Rabitsch W (2002) *Neobiota in Austria. Report of the Environment Agency Austria (in german)*. Vienna, Austria.
China	Jiang H, Fan Q, Li J-T, Shi S, Li S-P, Liao W-B, Shu W-S (2011) Naturalization of alien plants in China. *Biodiversity and Conservation*, **20**, 1545–1556.
Chile	Fuentes N, Pauchard A, Sánchez P, Esquivel J, Marticorena A (2013) A new comprehensive database of alien plant species in Chile based on herbarium records. *Biological Invasions*, **15**, 847–858.
Greece	Arianoutsou M, Bazos I, Delipetrou P, Kokkoris Y (2010) The alien flora of Greece: taxonomy, life traits and habitat preferences. *Biological Invasions*, **12**, 3525–3549.
India	Khuroo AA, Reshi ZA, Malik AH, Weber E, Rashid I, Dar GH (2011) Alien flora of India: taxonomic composition, invasion status and biogeographic affiliations. *Biological Invasions*, **14**, 99–113.
Italy	Celesti-Grapow L, Alessandrini A, Arrigoni PV *et al.* (2009) Inventory of the non-native flora of Italy. *Plant Biosystems – An International Journal Dealing with all Aspects of Plant Biology*, **143**, 386–430.
Portugal	De Almeida JD, Freitas H (2006) Exotic naturalized flora of continental Portugal – A reassessment. *Botanica Complutensis*, **30**, 117–130.
Singapore	Corlett RT (1988) The naturalized flora of Singapore. *Journal of Biogeography*, **15**, 657–663.
Taiwan	Wu S, Yang TYA, Teng Y, Chang C, Yang K, Hsieh C-F (2010) Insights of the latest naturalized flora of Taiwan: change in the past 8 years. *Taiwania*, **55**, 139–159.
Uruguay	Masciadri S, Brugnoli E, Muniz P (2010) InBUy Database of Invasive and Alien Species (IAS) in Uruguay: a useful tool to confront this threat to biodiversity. *Biota Neotropica*, **10**, 205–214.
Zimbabwe	Maroyi A (2012) The casual, naturalised and invasive alien flora of Zimbabwe based on herbarium and literature records. *Koedoe*, **54**, 1–6.

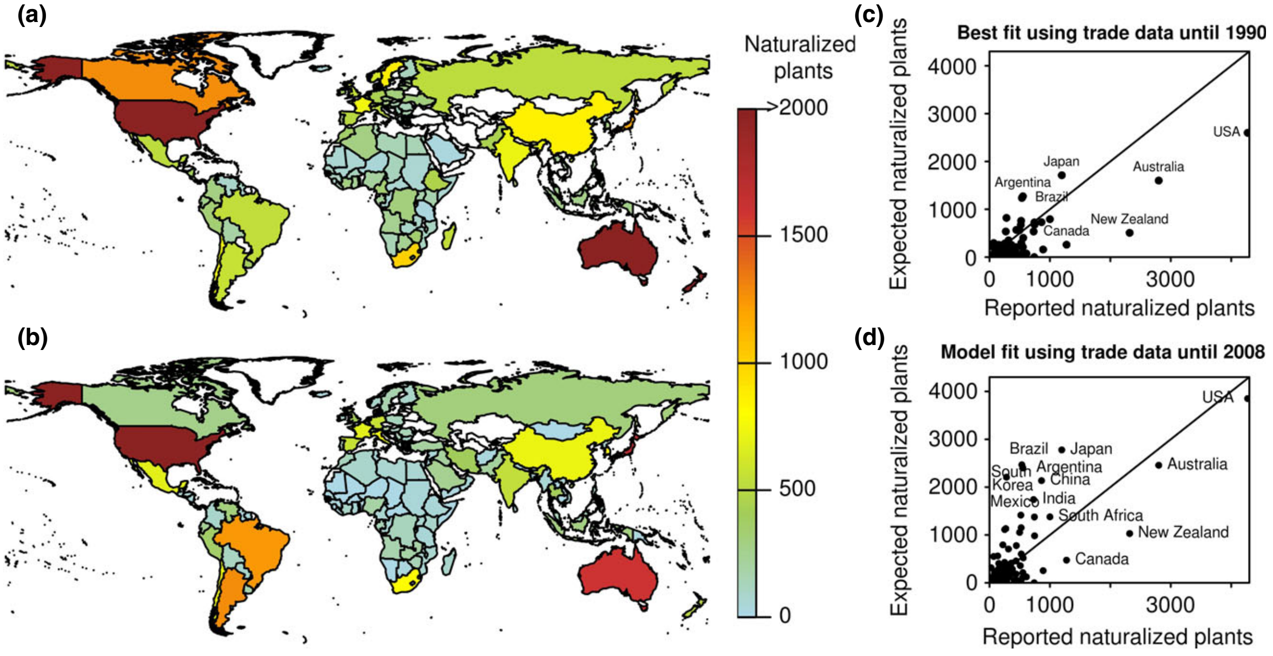

Fig. 1 Comparison of (a) reported (for 119 countries) and (b) predicted (for 147 countries) numbers of naturalized plants. Predicted numbers of naturalized plants represent mean values of 100 parameterizations of randomly selected subsets of 80% of the training data set. Countries in white are lacking species inventories. (c) Relationship of reported and predicted naturalized plant numbers using trade data until 1990 which represents the best fit. Countries such as the United States, Australia, New Zealand, and Canada were underpredicted, likely due to their specific colonial history not addressed in the model. (d) Using most recent trade data (until 2008), predicted naturalized plant numbers are higher than observed ones in emerging economies as their recent increase in trade is not yet fully reflected in the total number of naturalized plants.

GloNAF, emphasis was on obtaining data of naturalized alien plants in individual regions that was as complete as possible, following the standard criteria for a naturalized species as one that reproduces in the wild for a long period of time without help of the humans, and forms therefore a permanent part of the local flora (Richardson *et al.*, 2000; Pyšek *et al.*, 2004; Blackburn *et al.*, 2011).

Robustness analysis

To test the robustness of our model results, we performed a comprehensive sensitivity analysis. In particular, we did the following:

1. Variation of model structure: We tested 11 different model versions incorporating different potential predictors of alien plant invasion and combinations of them (in addition to the one presented in the main text: ignoring native species numbers in the donor country or accounting for stepping-stone dynamics, seasonality, land use, country size, recent human migration flows, degree of endemism, the number of botanical gardens per country, which is a major pathway for plant introductions (Hulme, 2011) and their year of foundation, geographical isolation, or combinations of these factors) (Fig. S6).
2. Variation of parameter values: The parameter values identified by simulated annealing were varied over a pre-defined range to investigate their influence on model results (Fig. S7).
3. Alternative parameterization data set: To test the influence of the data set used for parameterization, we selected an alternative training data set of global flows of alien plant species obtained from the 'Global Invasive Species Database' (GISD, http://www.issg.org/database/welcome/), which provides native and alien ranges of 290 naturalized plants worldwide. The native and alien ranges were combined for each species to calculate the flows of alien species between source regions and a specific country. Model results calculated with both the original and the alternative data set were compared (see 'Sensitivity Analysis' in the Supporting Information).
4. Randomization of case studies: To test the influence of selected case studies, which were used for parameterization, we parameterized the model using just a randomly selected subset of case studies (Fig. S8).
5. Randomization of training data set: To test the influence of variation within the training data set, we randomly sampled a subset of the training data set and repeated the parameterization 100 times for the best-fitting model. The obtained mean and coefficient of variation of model predictions are presented in Fig. 1b and Fig. S9.
6. Alternative trade data set: As the bilateral trade data set represents the most important input variable for the model, we tested a second data set obtained from the 'Correlates of

War' (COW) project (Barbieri *et al.*, 2009). The COW data set was used to test the robustness of the results and to investigate the influence of pre-1948 trading activities while considering import volumes from 1900 to 2008.

Furthermore, we provide a list of model assumptions and their influences on the results (see Supporting Information for the details of the sensitivity analysis).

Results and discussion

Parameterizing the model revealed that the best-fitting model can reproduce the reported flows of naturalized plants of the training data set very well (all studies: median of Pearson's $r = 0.80$), albeit with a large variation, ranging from $r = 0.15$ for Zimbabwe to $r = 0.97$ for Argentina (Fig. S10). The low congruence between reported and predicted naturalized plants for some case studies mainly results from single combinations of native and alien regions, which were underpredicted by the model. For instance, naturalized plant numbers for Austria are well reproduced except for those species originating from the Mediterranean. The high number of these reported short-distance introductions of naturalized plants is likely a consequence of the interaction of the high similarity of habitats in the lowlands of southern Central Europe and submediterranean regions (which are included in the Mediterranean region) and dispersal limitation due to the Mediterranean Sea and the Alps. Intensified trading activities during the last century enabled species to overcome these dispersal barriers and the concomitant increase in temperatures allowed them to survive in the new habitats (Essl & Rabitsch, 2002; see Pyšek *et al.*, 2012b for an example from the Czech Republic). Removing the naturalized plants originating in the Mediterranean region from the analysis increased the correlation between reported and predicted naturalized plants for Austria from $r = 0.38$ to $r = 0.87$.

Testing the model results using the data set of naturalized plant numbers of 119 countries shows that the predicted numbers of naturalized plants concur well with observed numbers (mean Pearson's r ± standard deviation: 0.78 ± 0.04; the mean and standard deviation are calculated from 100 repeated parameterizations of randomly chosen subsets (80%) of the training data set, Fig. 1a,b). Obvious outliers are the United States, Australia, New Zealand, and Canada (Fig. 1c), which, however, were excluded from the model parameterization. These countries were underpredicted by the model, which is most likely a consequence of their colonial history. They were former colonies that were populated by large numbers of Europeans during the last centuries. For example, during 1500–1965, the transatlantic migration to the USA and Canada was 2.5 times greater than migrations to Argentina and Brazil (Keeling, 2013), probably resulting in the introduction of many species of European origin to North America (Di Castri, 1989; Winter *et al.*, 2010). As these introduction waves are not related to trade in the last 60 years, they cannot be captured by our model.

Directionality in global flows of alien plants: revisiting the imperialist dogma

Our analysis indicates a distinct directionality in the global flows of naturalized plants between regions (Fig. 2, see also Fridley, 2013). The model predicts that, by far, the greatest flow of alien plants that successfully naturalized was from Asia to Europe (Fig. 2, Table S1). This directionality is mainly a consequence of the asymmetric exchanges of commodities between regions as, for example, Europe imported 19% more goods from

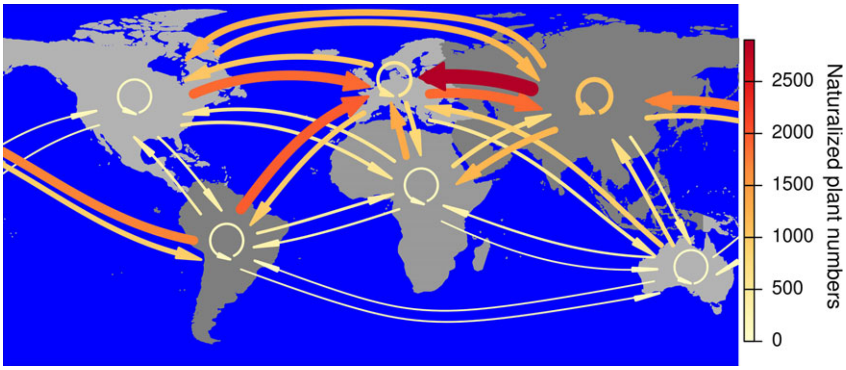

Fig. 2 The global network of naturalized plant invasion. The arrows indicate the modeled spread of plant species between continents (marked in different shades of gray), which established in the new region, while the width and the color of the arrows scale with the predicted number of naturalized plants. Plant invasions between countries of the same continent are shown by loops. The numbers of naturalized plants exchanged between continents are presented in Table S1.

Asia during the time period under investigation than it exported to Asia (Gleditsch, 2002). In total, model results show that Europe has a positive net naturalized plants balance; that is, the imports of plant species during the last 60 years are considerably higher than the exports (ratio of imports to exports: 1.7). In comparison, Asia imported nearly as many naturalized plants as it exported (import/export ratio: 0.94), while the exports from North America exceeded the imports (import/export ratio: 0.81). This contrasts with the common belief that Europe is still a net exporter of naturalized plants, a phenomenon known as the 'imperialist dogma' (Drake *et al.*, 1989). However, the 'imperialist dogma' mainly arose from trade activities in colonial times, whereas we use post-1948 trade data. Thus, our results show that the direction of spread of naturalized plants has changed from colonial times to recent times.

Our model results suggest that global trade plays a crucial role for the global flows of naturalized plants, and indeed, excluding trade values from the model strongly reduces the goodness of fit between reported and predicted naturalized plant numbers per country ($r = 0.37$). A comparison of model results with and without trade using Akaike's information criterion (AIC) revealed a difference of $\Delta\text{AIC} = 464$, indicating a very strong support for the model incorporating trade as a predictor variable (note that models with $\Delta\text{AIC} > 10$ have essentially no support *sensu* Burnham & Anderson, 2004). This supports previous findings that the number of established alien species is significantly correlated with the import value of a country (Levine & D'Antonio, 2003; Westphal *et al.*, 2008). However, in the model, the global flows of naturalized plants do not only vary due to variations in trade value but also because of differences in the numbers of potential invaders in the source regions or varying habitat suitability. To test this, we normalized the imports of naturalized plants to a country by the import value of that country, thereby identifying the global patterns of plant invasions independent of trading activities (Fig. 3). Highest mean imports of naturalized plants per import value were predicted for Australia (15 species per billion $US), Mexico (15), Thailand (14), and India (12), whereas lowest numbers were predicted for the northernmost countries such as Russia (0.5), Canada (1.0), and Finland (2.0). As the predicted number of naturalized plants per import value depends only on environmental conditions and native species numbers, the high predicted values in (sub)tropical countries can only result from the fact that these countries provide similar climatic conditions and harbor a large number of native species, which can be potentially introduced to another (sub)tropical country. In contrast, the lower richness of species in temperate climates results in a lower number of species per monetary unit with the potential to be introduced to other temperate countries. In reality, however, the existence of such a latitudinal gradient of the flows of naturalized plants per import value remains to be tested.

The implementation of historical trade data allows us to analyze lagged responses between the import of commodities and the naturalization of alien plant species. Similar to a cross-correlation analysis, we calculated the deviations expressed as the RMSE between model predictions of a certain year and observed species number, N_{ij}(Inv), as described in 'Materials and methods.' As the sampling periods of the 119 naturalized plants inventories ended on average at 2010 and the trade data ranged from 1948 to 2008, we considered time lags from 2 to 62 years. The lowest deviation of observed and predicted data was found at 1990 (Fig. 4). That is, the current total numbers of naturalized plants can be best explained by cumulative trade value data until 1990. Thus, the average lag time until increasing trade values manifest themselves fully in naturalized plant numbers is at least 20 years resulting in an 'invasion debt' (Essl *et al.*, 2011) of two decades. Using trade data until 2008 resulted in an increase in predicted

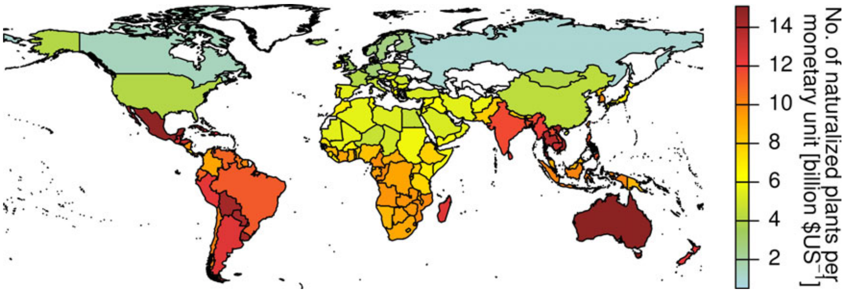

Fig. 3 The mean import of naturalized plants per monetary unit of trade during 1948–1990. For each link between country *i* and *j*, the number of expected naturalized plants, E_{ij}(Inv), is divided by the amount of trade (in US$) G_{ij} and averaged over all incoming links to country *j*: $\bar{E}_j(\text{Inv}) = \sum_i [E_{ij}(\text{Inv})/G_{ij}]/n_j$ with n_j being the number of trading partners of country *j*.

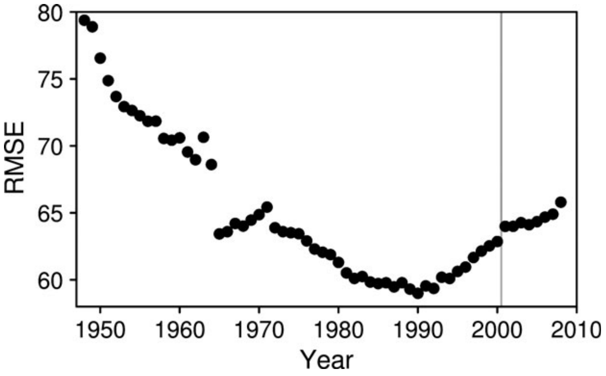

Fig. 4 Time-lagged response between socioeconomic activities and the reported number of naturalized plants. The figure shows the development of the deviations between reported and predicted naturalized plants measured as the RMSE for increasing time periods (1948 to the year shown on the x-axis) of cumulative annual bilateral trade. The best fit was found using the sum of trade value from 1948 to 1990. As the number of naturalized plants is reported on average from 2010, this indicates a time-lagged response between increases in trade and the resulting increase in reported naturalized plant numbers of around 20 years. The goodness of fit is given as the root-mean-squared deviation between model predictions and reported number of naturalized plants per country. Trade data until 2000 were taken from Gleditsch (2002) and from 2001 to 2008 from Barbieri *et al.* (2009) (separated by the vertical gray line).

naturalized plant numbers of all countries as the import value increased for all countries as well. For China, Argentina, South Korea, Brazil, India, Mexico, and South Africa, the usage of recent trade data revealed distinct overpredictions (Fig. 1d). These emerging economies have experienced a particularly strong recent increase in trade values, which currently is not fully reflected in documented naturalized plant numbers. A lag time of 20 years seems to be low compared to lag times of 100 years and more reported in other studies (Kowarik, 1995; Caley *et al*., 2008). However, the lag time identified in this study represents the time delay between increases in trade value and manifested increases in naturalized plant numbers. The lag time defined by Kowarik (1995) is the time period between first introduction of a species and its first recorded escape from cultivation, while Caley *et al.* (2008) define lag time as the time period between the first record in the new environment and the time of naturalization. Thus, the definitions of a lag time differ and the results are not directly comparable among the studies. In addition, the studies of Kowarik (1995) and Caley *et al.* (2008) focus on woody plants, which have longer generation times than most herbaceous species also considered here.

Invasion debt: a ticking time bomb for emerging economies

Global trade increased from 1990 to 2008 fivefold (Barbieri *et al*., 2009), which should cause a distinct increase in naturalized plant species numbers too. To quantify this increase, we applied a conservative approach and used a lagged response of two decades between trade and naturalized plant numbers. We took advantage of the observed time lag of 20 years between the increases in trade value and naturalized plant numbers and used the most recent trade data to predict naturalized plant numbers in 20 years. More precisely, we ran the model, which was parameterized to cumulative trade value data from 1948 to 1990, but using trade values from 1948 to 2008 to predict country-specific trajectories of naturalized plant numbers until 2028. Highest increases in absolute numbers of naturalized plants are expected for South and East Asian countries (South Korea, India, Thailand, and China) but also for Argentina, Brazil, Australia, and the United States (Fig. 5a). Accounting for the varying amount of imports revealed that the largest increases in naturalized plants per import value are expected for emerging economies (Fig. 6). Although the increase in trade value for these countries is a magnitude lower than those observed for the USA and China, the number of new naturalized plants is predicted to be the same or even higher. The greatest relative increases in naturalized plant numbers are predicted for small African and South-East Asian economies with a strong relative increase in trade during the last decades (Fig. 5b).

New establishments of alien species should be influenced by changes in habitat suitability due to climate change (Walther *et al*., 2009). To investigate the interacting influence of climatic changes and increases in global trade on future biological invasions, we ran our model based on current climate and, alternatively, incorporating projected future changes in temperature and precipitation in the recipient country. We found substantial differences between the predictions with and without climate change. For example, Brazil is expected to be invaded by 88 fewer species, while the United States is predicted to be invaded by 56 more species due to climate change (Fig. 5c). In contrast to other studies (Walther *et al*., 2009; but see Bellard *et al*., 2013), our model shows a strong latitudinal gradient of the influence of climate change on the expected numbers of naturalized plants (Fig. 5d). Temperate regions of the Northern Hemisphere are predicted to be more strongly invaded by aliens under climate change, while countries in the (sub)tropics and in the Southern Hemisphere will be less invaded. In temperate regions, rising temperatures will increase the environmental match

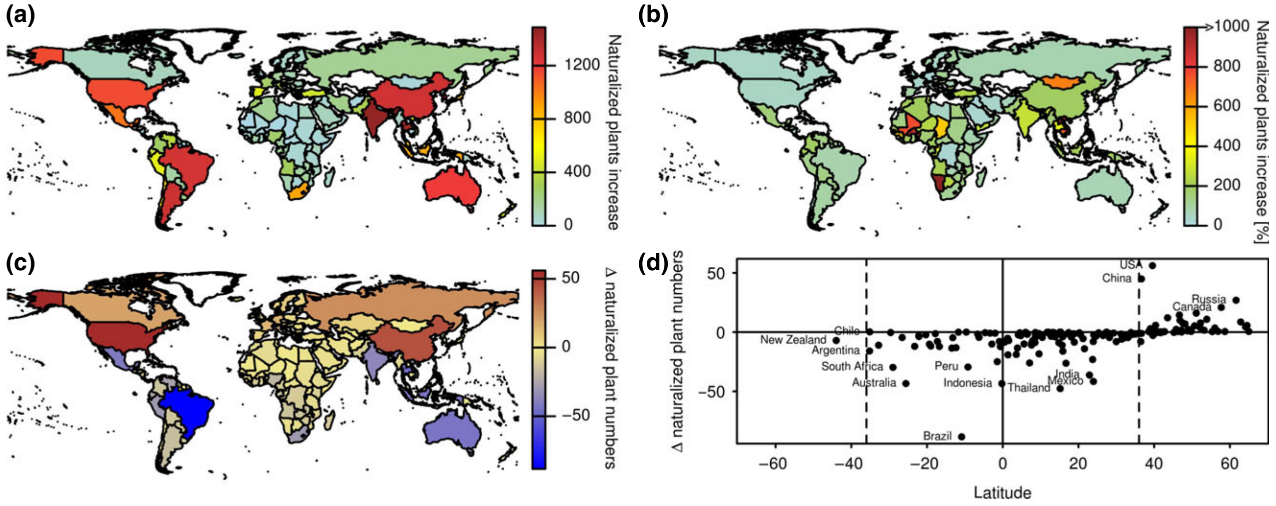

Fig. 5 The predicted increase in naturalized plants per country until 2028. The (a) absolute and (b) relative differences of recent and future naturalized plant numbers under the consideration of a constant climate. (c, d) Differences in the predicted number of naturalized plants with and without the consideration of climate change. Positive values indicate an increase in species numbers under climate change and negative values a decrease. Temperate regions of the Northern Hemisphere (north of the 38° parallel, vertical dashed line in d) are predicted to receive more naturalized plants under climate change, while countries in the (sub)tropics and on the Southern Hemisphere will be less invaded.

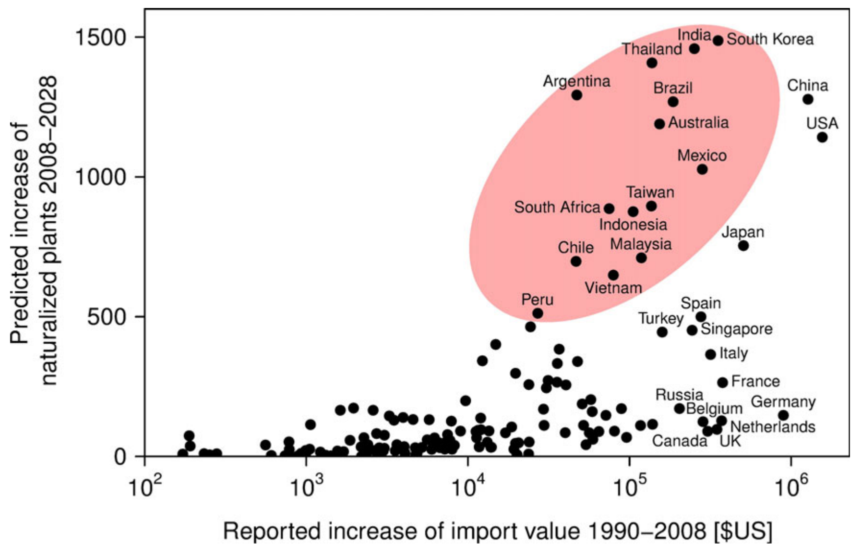

Fig. 6 Relationship between the increase in import value (1990–2008) and the predicted increase in the number of naturalized plants until 2028. The red area (drawn by hand) highlights those countries with highest predicted increases in naturalized plants and comparatively low increases in import values. Most of these countries belong to the emerging economies.

with species-rich subtropical regions (Walther *et al.*, 2009). In contrast, further warming in tropical and subtropical regions is predicted to decrease the climatic match with current major source countries for alien plant species (see also Bellard *et al.*, 2013). However, the numbers of naturalized plants predicted to vary due to climate change are comparatively low compared to predicted increases due to rising imports within the last two decades. Thus, the potential reduction in naturalized plant numbers due to climate change in some countries is too small to cancel out the trade-related increases.

In addition to the predicted increase in mean annual temperature and precipitation, the variability of these parameters is predicted to increase as well (Settele *et al.*, 2014). The greater environmental variability may modify the future number of naturalized plants. This is because the chance of naturalization may either become higher for warm-adapted species as they are able to survive the critical initial steps of invasion during warm periods, or it may become lower due to less stable environments. The role environmental variability plays in the macroecology of biological invasions remains to be analyzed in subsequent studies. It has to be noted that the predicted numbers of naturalized plants represent mean values averaged across the entire distribution of a species, although in nature the dynamics are more complex due to central–marginal population dynamics (Guo, 2014). At the center of a species' distribution, the density tends to be high and, thus, a population is more robust against disturbances compared to a population at range margins, where densities are lower. Consequently, populations of the same species may respond differently to climate change depending on their densities.

Model uncertainties: an evaluation of data quality and model formulation

Model results are mainly affected by two types of uncertainties: (i) sampling errors and biases of the underlying data and (ii) uncertainties in the correct model formulation. To test the robustness of our model predictions, we performed an extensive sensitivity analysis (see Supporting Information), results of which are summarized as follows: We first analyzed the influence of data quality on model predictions. The backbone and, thus, an influential part of our model are the data set of bilateral trade values. To investigate its influence on model results, we applied the same model fitting using a second data set (Barbieri *et al.*, 2009), which, however, revealed nearly the same model results (correlation of predicted naturalized plants using both data sets: $r = 0.99$). Hence, although both trade data sets deviate in the number of considered country pairs (Fig. S2), these differences do not affect the model output. This trade data set spans a larger time period – though for fewer countries – allowing us to test the influence of pre-1948 trade while including import volumes from 1900 to 2008. Again, the changes are marginal (correlation of predicted naturalized plants using both data sets: $r = 0.99$), indicating that for the cumulative sum of trade values until 1990, pre-1948 trade values do not play a significant role. Model results are highly dependent on the selected values of the model parameters, which were identified by fitting the model to the training data set. To test the influence of the training data set on model results, we used the GISD data as an alternative training data set to parameterize the model. The usage of GISD data revealed a reduced congruence of predicted and reported naturalized plant numbers ($r = 0.55$ compared to $r = 0.78$ using our training data set), probably because GISD focuses on species posing harm to the environment, and therefore contains a comparatively low number of species. We therefore decided to apply the data set which yields the best fit of reported and predicted numbers. The parameter setting identified in this way seemed to be robust as moderate changes (<30% of the values) affected the model output only marginally (Fig. S7).

To address the second major source of model uncertainty (i.e., model formulation), we formulated 10 additional model versions considering further major drivers for the spread of alien plants such as the distribution and age of botanical gardens, stepping-stone dynamics, seasonality, recent human migration, and land use (see Supporting Information). Compared to the model versions provided in the main text, all other modifications revealed either the same or a larger deviation of observed and predicted values (Fig. S6). We therefore selected the simplest model version among the best-fitting ones as the main model. We list and discuss further model assumptions in the 'Sensitivity Analysis' in the Supporting Information. Despite the large number of model modifications tested in this study, some important drivers are still missing such as biotic interactions and historical human migration. Biotic interactions, however, are highly specific to a species, to the respective region where the species is introduced, and to the time of introduction. In addition, general rules defining the influence of biotic interactions on invasion dynamics are still lacking or hotly debated such as the 'biotic resistance hypothesis' (Kennedy *et al.*, 2002; Fridley *et al.*, 2007). It is therefore very difficult to incorporate biotic interactions in a global modeling study, which explicitly neglects the consideration of species-specific traits. The implementation of historical human migration is hampered by the lack of data. For a few large regions, data are sparsely available (Keeling, 2013), and comprehensive data on a global scale are provided only for recent time periods (1990–2010, Abel & Sander, 2014). However, the incorporation of recent human migration flows did not improve the model results probably due to their low influence on plant invasions in modern times (Fig. S6). A general challenge for models dealing with habitat suitability such as the one presented here or for species distribution models is the sufficient description of the habitat of species (Elith & Leathwick, 2009). Here, we used annual averages of environmental variables of countries, thus neglecting the spatial and temporal variation within a country. Consequently, two countries may appear to be more similar or more dissimilar than they are in reality. The consideration of seasonality is a straightforward approach to account for temporal variation but it still neglects temporal (mis-)matches of two habitats. However, as there is currently no best-practice solution for the correct estimation of habitat suitability from distributional data, we applied a conservative approach of using mean values of the three most important environmental parameters.

Predicting the trajectories of future plant invasions

For the first time, this study analyzes the role of the trade network, environmental factors, and their interactions with climate change on global terrestrial invasion patterns of a major taxonomic group. Our results show that the global trade network plays a pivotal role in driving variations in levels of terrestrial plant invasion. However, the biogeographic and climatic position of the recipient country modulates the average number of naturalized plants per import value, with many subtropical and tropical countries receiving by more than an order of magnitude more naturalized plants per unit of import value than boreal and temperate Eurasian countries. Accounting for temporal changes in trade intensity showed that lag times between increases in trade value and alien species accumulation (‘invasion debt’) are substantial, although they are shorter than those found in previous studies (Essl *et al*., 2011). The current distribution of naturalized plants reflects past socioeconomic activities, and consequently, recent strong increases in trading activity will cause substantial increases in invasion levels within a few decades, particularly in emerging economies, which show most pronounced growth of naturalized plant numbers compared to countries with similar trade value increases (Fig. 6). Alarmingly, most of these economies coincide with megadiverse regions (Brooks *et al*., 2006), rich in endemic and rare species. Climate change will modify future levels of invasions as the intensity and direction of this interaction strongly depend on the latitudinal position of the focal country.

The global trade network has increased enormously since World War II in terms of the total value of exchanged goods. The technological development of means of transportations (e.g., large-scale transport of goods by airplanes, transcontinental containerships) has decreased the time necessary for intercontinental transport from weeks to days and greatly expanded the type and value of goods (and associated potential alien species) transported. As a consequence, trade has remained the unrivaled cause of the intentional and unintentional introduction of alien species (Hulme, 2009). Although an increasing number of national and international regulations and import inspections aimed at reducing the unwanted introduction of invasive species have been put in place during the last decades (Hulme, 2006), the overall level of propagule pressure associated with trade does not seem to have decreased. Due to time lags, the consequences of recently adopted alien species policies aiming to halt the introduction of new alien species may only become discernible after decades. By contributing to the understanding of interactions of global drivers of invasions, such as trade and climate change, and identifying regions that are likely to suffer the greatest risk from plant invasions in the near future, this study provides a foundation for a much improved knowledge of the causes and trajectories of global plant invasions. This is a pivotal prerequisite for the effective management of biological invasions (Hulme *et al*., 2008). The results clearly demonstrate the necessity of incorporating the issue of biological invasions in trade legislation and to foster international collaborations with regard to detecting new invasive species. Regions facing high risks of receiving new invaders should especially become the target of international policymaking.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Text S1. Detailed description of model parameterization.
Text S2. Sensitivity analysis.
Text S3. List and discussion of major model assumptions.
Figure S1. Temporal development (1948–2009) of exchanged trade volumes.
Figure S2. Temporal development of the sizes of the two bilateral trade data sets.
Figure S3. Visualization of data used as predictor variables in model.
Figure S4. Predicted future increases in annual mean temperature and annual mean precipitation.
Figure S5. Intercorrelations of the probabilities P(Alien), P(Intro) and P(Estab).
Figure S6. Temporal development of goodness-of-fits for various model modifications.
Figure S7. Influence of changes of parameter values on model results.
Figure S8. Influence of the number of selected case studies (3–11 studies) on model accuracy.
Figure S9. Variation of model predictions for each country.
Figure S10. Predicted and reported number of naturalized plants of the 12 case studies used for parameterization.
Figure S11. Temporal development of the Pearson's correlation coefficient between the two bilateral annual trade data sets.
Table S1. The total number of naturalized plants transported from a donor region to a recipient region.