Climate and socio-economic factors explain differences between observed and expected naturalization patterns of European plants around the world

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Research paper

Climate and socio-economic factors explain differences between observed and expected naturalization patterns of European plants around the world

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Data availability statement

The data used to build the species distribution models (occurrence records and environmental variables) came from openly accessible repositories cited in the manuscript (for details on the EVA database, see http://euroveg.org/eva-database-obtaining-data). All 1,485 generated habitat suitability raster files are available at https://dataverse.ird.fr/dataset.xhtml?persistentId=doi:10.23708/RNGS8Z.

Research paper

Climate and socio-economic factors explain differences between observed and expected naturalization patterns of European plants around the world

Running title: Observed versus expected naturalizations

Abstract

Aim – The number of naturalized (i.e., established) alien species has increased rapidly over the last centuries. Given the differences in environmental tolerances among species, little is known about what factors determine the extent to which the observed size of the naturalized range of a species and hence the extent to which the observed richness of naturalized species of a region approach their full potential. Here, we asked which region- and species-specific characteristics explain differences between observed and expected naturalizations.

Location – Global.

Time period – Present.

Major taxa studied – Vascular plants.

Methods – We determined the observed naturalized distribution outside Europe for 1,485 species endemic to Europe using the GloNAF database and their expected distributions outside Europe using species distribution models. First, we investigated which of seven socio-economic factors related to introduction pathways, anthropogenic pressures and inventory effort best explained the differences between observed and expected naturalized European floras. Second, we examined whether distributional features, economic use and functional traits explain the extent to which species have filled their expected ranges outside Europe.

Results – In terms of suitable area, more than 95% of expected naturalizations of European plants were not yet observed. Species were naturalized in only 4.2% of their suitable regions outside of Europe (range filling) and in 0.4% of their unsuitable regions (range expansion). Anthropogenic habitat disturbance primarily explained the difference between observed and expected naturalized European floras, as did the number of treaties relevant to invasive species. Species of ornamental and economic value and with large specific leaf area performed better at filling and expanding beyond their expected range.

Main conclusions – The naturalization of alien plant species is explained by climate matching but also by the regional level of human development, the introduction pressure associated with the ornamental and economic values of the species and their adaptation to disturbed environments.

Keywords – Alien species, anthropogenic pressure, environmental driver, functional trait, global change, introduction pathway, naturalization, ornamental plant, sampling bias, species distribution model.

Introduction

Species that maintain self-sustaining populations outside their native range independently of direct human intervention (i.e., naturalized species; Richardson *et al.*, 2000; Blackburn *et al.*, 2011) pose a serious concern to native biodiversity and ecosystem functioning and services worldwide (IPBES, 2019). Their number has increased substantially over the last few centuries and does not show any indication of saturation (Seebens *et al.*, 2017). Regions differ considerably in their richness of naturalized species of vascular plants, and species vary considerably in their extent of naturalization (Pyšek *et al.*, 2017, Essl *et al.*, 2019). Part of this variation may result from regional differences in the size of the potential naturalized alien pool and the size of the range potentially available for naturalized species. Little is known about the relationship of the observed and potential richness of naturalized plant species (i.e. the maximum numbers of alien species that these regions could host given species' environmental tolerances; Stohlgren *et al.*, 2008).

The actual distribution of naturalized alien plant species results from the number of introductions by humans (intentional or not) followed by the interplay of factors that determine the environmental space available for a species and factors that prevent or promote the extent to which an equilibrium with an environmental space is reached. Environmental suitability (e.g., climate, habitat) determines the potential (expected) distribution range by filtering the subset of introduced species that can maintain populations over long periods by successfully reproducing, i.e., naturalized species (Richardson & Pyšek, 2012). Human activities can further influence the observed distribution range of species by altering environmental conditions and dispersal processes that dictate opportunities for introductions. For instance, human transport, trade and increasing urban development tend to broaden observed ranges, while, conversely, biosecurity responses can contain this expansion (Hulme, 2009).

An increasing body of literature is investigating what proportions of species' potential alien ranges are actually occupied (Petitpierre *et al.*, 2012; Strubbe *et al.*, 2013, 2015; Hill *et al.*, 2017; Liu *et al.*, 2020). Indeed, most alien species are occupying only a subset of the niche corresponding to suitable environments that are occupied in their native range ('niche filling'). Certain alien species are also able to colonize new environments that are not occupied in their native range ('niche expansion'). Patterns of niche filling and niche expansion vary highly depending on the type of organisms. For instance, the average niche filling was found to be 80% for vascular plants considered invasive (i.e., spreading into areas away from sites of introduction; Richardson *et al.*, 2000), 37% for invasive insects and 20% for invasive birds, whereas the average niche expansion was 26% for birds, 20% for insects and 5% for plants (Petitpierre *et al.*, 2012; Strubbe *et al.*, 2013; Hill *et al.*, 2017). Niche changes during invasions appear to be primarily driven by introduction history (e.g., propagule pressure and colonization processes) in birds, and by human disturbance in insects (Hill *et al.*, 2017). However, little is known about what causes possible differences between observed and expected ranges in naturalized plants.

Much of the research effort has been devoted to understanding the socio-economic drivers of the number of naturalized alien plant species (Pyšek *et al*., 2010; van Kleunen *et al.*, 2015; Dawson *et al.*, 2017; Essl *et al.*, 2019), some of them focusing on the subset of invasive species (Essl *et al.*, 2015; Bellard *et al.*, 2016). However, studies dealing with alien species richness always face the challenge of disentangling the specific role of socio-economic drivers from that of large-scale biogeographical factors also known to influence species richness, irrespective of species origin (e.g., latitudinal gradient, resource availability). Moreover, while it is recognized that environmental matching between native and alien ranges largely controls naturalization (Richardson & Pyšek, 2012; Feng *et al.*, 2016), focusing on alien species richness does not allow accounting for species-specific environmental requirements. Hence, determining the expected distributional range of naturalized species should be an important step in understanding the influence of socio-economic factors on observed patterns of naturalization (Xu *et al.*, 2019).

Another advantage of analyzing species composition is that it allows for the identification of the species that explain the pattern of naturalized species richness and their characteristics. Many other studies have attempted to determine which species' performance or natural distribution traits are associated with naturalization success by comparing naturalized and non-naturalized plant species (e.g., Pyšek & Richardson, 2007; van Kleunen *et al.*, 2010; Pyšek *et al.*, 2015). Conclusions from these studies delivered little consensus and often appear to be context- and species-dependent. This might partly be because these studies only investigated trait differences of native versus alien or non-invasive versus invasive species (i.e., a binary variable), or tested for relationships between traits and the observed naturalized range without considering the potential range. Therefore, we believe we can gain additional insight into the drivers of naturalization patterns by searching for traits that explain the extent to which species fill or expand beyond their suitable alien range (i.e., a continuous variable that accounts for the potential range).

Europe is the second-most important donor continent of naturalized alien plant species, after Asia. However, the European flora is by far the most successful in naturalizing. Of the ~14,200 vascular plant species native (i.e. both endemic and non-endemic) to Europe, 3,383 have become naturalized somewhere in the world; this is three times more than expected by chance (van Kleunen *et al.*, 2015). Furthermore, five of the 10 globally most widely naturalized species are native to Europe (Pyšek *et al.*, 2017). The European flora is therefore suitable for studying drivers of differences between observed and expected naturalized ranges.

Current knowledge of which region- and plant-related characteristics influence the extent to which species fill their expected naturalized ranges is poor and relies only on the search of the socio-economic drivers of niche/range filling of a few invasive alien species (usually < 50;

e.g., Hill *et al.*, 2017; Petitpierre *et al.*, 2012; Strubbe *et al.*, 2013, 2015). However, the drivers of niche/range filling have never been explored for naturalized species (a much broader group of species than invasives; Richardon *et al.*, 2000); yet the processes driving the ability to survive and reproduce are likely to differ from the processes driving the spread and impact of invasive species (e.g., Abellán *et al.*, 2017). Moreover, the drivers of the difference between observed and expected naturalized regional floras (and not between observed and expected distributions of a few individual species) have never been explored.

In this study, we focused on 1,485 plant species endemic to Europe, an unprecedented number for this type of study, which allowed us to analyse in more detail what explains variation in the differences between observed and expected values. We determined both their current observed distribution in 931 non-European regions using the 'Global Naturalized Alien Flora' database (GloNAF; van Kleunen *et al.*, 2019) and their expected distribution using biogeoclimatic ensemble species distribution models (SDMs). We also explored which socio-economic factors explain why some regions have a recorded naturalized flora of European origin close to their expected naturalized flora, while other regions have not. Finally, we examined whether species distribution patterns, economic uses and functional traits explain why some species fill a larger portion of their expected range than others do.

Materials and methods

Expected naturalized ranges

Species selection

Many plant species native to Europe are also native to other continents such as Asia and Africa, for which there is usually a lower density (temporal and spatial) of species occurrence records (Meyer *et al.*, 2016). Therefore, we focused on vascular plant species whose native range is restricted to Europe (European endemics), as this allows us to better capture the full realized niche of the species in their native range. The physiography of the European continent was defined as bordered by the Arctic Ocean to the north (Iceland and Norwegian

Islands were included, Greenland was excluded), the Atlantic Ocean to the west (the British and Irish Isles were included and the Macaronesian archipelagos were excluded), the Ural Mountains, the Ural River, and the Caspian Sea to the east, and the Caucasus and the Mediterranean Sea to the south (Mediterranean islands were included, Anatolia was excluded).

The database 'Endemic vascular plants in Europe' (EvaplantE; Hobohm 2014), which comprises a list of > 6,200 endemic taxa, was used as a baseline for species selection. Scientific names were standardized based on a working list of all plant species (The Plant List; TPL; http://www.theplantlist.org/ version 12-10-2018). This taxonomic standardization was done with the R package 'Taxonstand' (Cayuela *et al.*, 2017). Standardized infraspecific taxa were excluded from the list, resulting in 4,965 species (Figure 1).

Compilation of species occurrence records

To comprehensively describe the distribution of the species in Europe (which in addition to the native range might for some species also include part of their alien range), we combined occurrence records from six sources (see Supporting Information Appendix S1 for details and references): the 'Global Biodiversity Information Facility' (GBIF), the 'European Vegetation Archive' (EVA; Chytrý *et al*., 2016), the 'EU-Forest' dataset, the 'Atlas Florae Europaeae', the 'Plant Functional Diversity of Grasslands' network (DIVGRASS) and the digital atlas of the German flora.

When several occurrence records from these different sources were duplicated on the same cell, only one occurrence record per species was kept to avoid pseudoreplication. Cell size was set to 0.42° × 0.42° (~50 km × 50 km at the equator) to approach the resolution of the source of occurrence records having the coarsest resolution (Atlas Florae Europaeae). Using a higher resolution (i.e., a smaller cell size) would have required to downscale this source of occurrence records, which typically introduces spatial biases and uncertainty in the model predictions (Bonbi & D'Amen, 2012). Moreover, this resolution appeared to be a good compromise to account for the fact that the selected environmental variables (climate, land use and soil type) determine invasion potential at different scales (10,000 to 200 km, 2,000 to 10 km, and 10 km to 10 m, respectively; Milbau *et al.*, 2009).

Species with fewer than 10 deduplicated occurrence records were not further considered since the resulting SDM might be inaccurate. The final dataset comprised 135,189 occurrence records for a total of 1,485 European plant species, belonging to 327 genera and 67 families (Table S1), i.e. on average 91 occurrence records per species with a maximum of 1,382 occurrence records for *Achillea ptarmica* (Asteraceae). We had enough occurrence records to build an SDM (i.e., 10 occurrences) for 272 European species among the 407 already naturalized species and for 1,213 species currently not known to be naturalized anywhere.

Environmental predictors of expected ranges

We defined six environmental variables to model and project species expected ranges. These variables were related to climate, land use, and soil physico-chemical properties, which are commonly recognized to shape the distribution of plants (Gurevitch *et al.*, 2006). Annual mean temperature (°C), annual precipitation (mm) and precipitation seasonality (yearly coefficient of variation) representing the period 1979-2013 were provided at a 30 arcsec resolution by the CHELSA climate database (Karger *et al.*, 2017). Worldwide correlations between these variables and the others described below did not exceed the threshold of $|r| = 0.70$ (Supporting Information Appendix Figure S1) beyond which collinearity begins to severely distort model estimations and subsequent predictions (Dormann *et al.*, 2013). However, these variables reflecting trends in average climate conditions were significantly correlated with climate extremes to which plants are recognized to be highly responsive (Zimmermann *et al.*, 2009). The percentage of each grid cell with primary land cover based on the Harmonized Global Land Use models was also used (Chini *et al.*, 2014). Organic carbon content (g per kg) and pH in the first 15 cm of soil were extracted at a 1 km resolution from the global gridded soil information database SoilGrids (Hengl *et al.*, 2014). Environmental variables were aggregated (using the mean value) to the resolution of 0.42° × 0.42°.

Species distribution modelling

Comparing the realized niche within the native versus alien ranges can lead to three cases: 1) in the alien range, the species uses a similar or smaller realized niche than in the native range, e.g., because of new competitors, herbivores or pathogens, or dispersal limitation; 2) the species occupies a realized niche very different from the one in the native area but within the species initial fundamental niche, e.g., because of new biotic interactions, multiple sites of introduction, niche differentiation or different environmental conditions; or 3) the realized niche extends outside of the species initial fundamental niche, e.g., because of rapid niche evolution, enemy-release or new positive interactions (see Gallien *et al.*, 2010 for further details). As options 2 and 3 remain impossible to predict for a large number of species, we only considered option 1 in this study.

The expected distribution of the 1,485 European plant species was modelled by statistically relating the environmental predictors to the distribution data in Europe. Six species distribution modelling (SDM) methods including generalized additive models, generalized linear models, generalized boosting trees, maximum entropy, multivariate adaptive regression splines and random forest were used. All of these methods require presence and absence or pseudo-absence/background data (a random subset of the available environmental conditions in the area, i.e., Europe in our case), whose selection can significantly affect predictions if not made adequately. Consequently, we performed a preliminary analysis to identify the most appropriate set of pseudo-absences for each SDM method (Appendix S2). The predictive performance of SDM in Europe was assessed by measuring the area under the receiver operating characteristic (ROC) curve (AUC) and the true skill statistics (TSS; Allouche *et al.,* 2006). AUC values can range from 0 to 1, an AUC of

1 indicating a perfect fit, an AUC of 0.5 meaning that predictions from SDM do not differ from random, and an AUC of 0 meaning the SDM is always incorrect. TSS ranges from −1 to 1, where 1 indicates perfect agreement and 0 indicates a random prediction.

To combine the predictive capability of the six SDMs, their projections were subsequently aggregated into an average or consensus projection. To ensure the quality of the ensemble SDM, we only kept the projections for which the accuracy estimated by AUC and TSS were higher than 0.8 and 0.6, respectively, and assembled the selected SDMs using a committee-average approach with each SDM was weighted proportional to its TSS evaluation. Probability maps obtained from the ensemble forecasting projections were then transformed into binary suitable/non-suitable maps using the threshold maximizing the TSS to ensure the most accurate predictions, since it is based on both sensitivity and specificity. The entire species distribution modelling workflow was performed within the 'biomod2' R platform (Thuiller *et al.*, 2009).

Recorded naturalized ranges

The current observed naturalized range of the European flora was obtained through the GloNAF database version 1.2, a recently compiled database of ~14,000 naturalized alien plant species covering 1,029 regions worldwide, corresponding to administrative regions such as countries, states and provinces, and also including 381 islands (van Kleunen *et al.*, 2019). The size of a region ranged from 0.03 km² (Tauna islet of the Gambier archipelago, French Polynesia) to 2,486,952 km² (the Republic of the Sudan plus South Sudan). A total of 407 European endemic species were found as naturalized in at least one of the non-European GloNAF regions.

We explored various definitions of suitability by analyzing what proportion of a region should be suitable for a species to become naturalized in this region. The following definitions were used: at least one suitable cell, 1%, 5%, 20%, 50%, or 100% suitable cells, respectively. For each region, species were classified into: true positives (TP), i.e., species that are both observed and predicted as being successfully naturalized in the region; false positives (FP), i.e., species that have not become naturalized, but are predicted as successfully naturalized; false negatives (FN), i.e., species that are observed as successfully naturalized but not predicted to be naturalized; and true negatives (TN), i.e., species that are neither predicted nor observed to be naturalized in the region. Then, the predicted naturalized species pool was compared to the observed naturalized pool by calculating: 1) the naturalization debt in the broad sense hereafter referred to as ‘naturalization debt’ (FP/(TP+FP)), i.e., the proportion of predicted naturalizations that are not yet observed either because species are not yet introduced to the focal area (introduction debt) or because they were introduced, but are not naturalized yet (naturalization debt in the strict sense, i.e., *sensu* Rouget *et al.*, 2016), which can take several decades or centuries for some taxa; 2) the assemblage sensitivity (TP/(TP+FN)), i.e., the proportion of observed naturalizations that are correctly predicted ; 3) the negative predictive value (TN/(TN+FN)), i.e., the proportion of species that were not predicted to be naturalized and have not become naturalized in the region.

Socio-economic drivers of naturalization patterns

Seven factors were extracted to explain naturalization debt, assemblage sensitivity and the negative predictive value (Table 1). These factors were selected because they provided insights into introduction pathways, human pressures and inventory effort: airport density (‘Airports’), seaport density (‘Seaports’), number of international treaties relevant to invasive alien species (‘Treaties’), human population density (‘Population’), proportion of croplands (‘Cropland’), human development index (‘Development’) and species inventory effort (‘Inventory’; for details, see Appendix S3). These socio-economic factors were independent of the surface area of the regions. They were available for 526 non-European regions including 17 islands or archipelagos and 509 mainland areas. Regional factors were tested for multicollinearity by computing a correlation matrix based on Pearson's r. Cross-correlations did not exceed $r = 0.51$ (between airport and seaport density), which is below the threshold of 0.70 (Figure S3; Dormann *et al.*, 2013).

Identification of the drivers of naturalization patterns was based on boosted regression trees (BRTs), a machine-learning method that combines a large number of relatively simple tree models to optimize predictive performance (Elith *et al.*, 2008). The quality of BRT fits was controlled with the coefficient of determination of the regression between estimated and observed values (r^2) and the standard error (se). Results were interpreted by looking at the relative influence of the seven regional socio-economic factors to the predictive models (calculated based on the number of times a factor is selected in the model, weighted by its improvement to the overall model) and by considering the partial dependence of the predictions on each factor after accounting for the average effect of the other factors.

Plant features explaining naturalization patterns

To assess which species-level features affect naturalization success, we first compared European species recorded as naturalized outside Europe ('naturalized') and those not recorded as naturalized outside Europe ('non-naturalized'). Eight features including two distributional indices, the economic use of the species and four functional traits were selected: 1) species prevalence in Europe measured as the number of 0.42° × 0.42° cells occupied; 2) the surface area of the species' expected range outside Europe. These distributional indices were used because more widespread species are usually hypothesized to have a greater potential to spread and a higher invasion success (Gallien *et al.*, 2019); 3) whether the species is used as an ornamental plant or 4) has other economic relevance (e.g., food plant, medicines, materials) according to the World Economic Plants (WEP) database (Wiersema & León, 2013) since the ornamental and economic relevance of a species is thought to be a key predictor of its probability to be introduced and its naturalization success (van Kleunen *et al*., 2018, 2020); 5) the growth form (i.e., graminoid, non-graminoid herb, shrub or tree), a major determinant of invasiveness (Pyšek & Richardson, 2007); 6) mean specific leaf area (SLA), i.e., the ratio of leaf area to leaf dry mass (expressed in $m^{-2} \cdot g$); 7) mean plant height (in m); and 8) mean seed mass (in g). These last three functional traits represent key axes of plant ecological strategies following the leaf–

height–seed (LHS) scheme of Westoby (1998). Correlation between LHS traits was $|r| < 0.27$. Functional traits were extracted from the TRY database (Kattge *et al.*, 2020). Linear mixed-effect models (LMMs) were fitted using a phylogenetic generalized least square approach (PGLS) to compare features of naturalized and non-naturalized species while controlling for between-species phylogenetic distances (for details on the phylogeny used, see Appendix S4). As we did not have data on all features for each species (see Figure 6), we ran separate LMMs for each of the eight features. LMMs were performed using the *gls()* function of the R package 'nlme' (Pinheiro *et al.*, 2019).

We used LMMs accounting for phylogeny to test whether plant-feature values explain: 1) the relative extent of range filling, i.e., the proportion of suitable regions where a species has become naturalized; and 2) the relative extent of range expansion, i.e., the proportion of unsuitable regions where a species has nevertheless become naturalized. The indices of range filling and expansion that we used are similar to the indices used by Petitpierre *et al.* (2012). However, we calculated them in the geographical space instead of in the environmental space because occurrence data on naturalized plants are not evenly comprehensive across regions (which would have been needed to offer a reliable fit of the niches), and when an alien species is reported, we do not always know whether or not it reproduces in the wild (Figure 1).

Results

Socio-economic drivers of naturalization patterns

European endemic vascular plant species have naturalized in 319 non-European regions. The naturalization debt (i.e., the proportion of species which are not yet naturalized in a particular region but likely to become so, if introduced, given their environmental envelope) ranged from 95 to 100% (mean = 99%) among the 931 non-European regions according to the threshold of one pixel and from 71 to 100% (mean = 99% as well) according to the threshold of 100% of suitable cells (Figure 2). This means that less than 5% and less than

29% of species for which a region is suitable according to the lowest and highest thresholds, respectively, have actually been recorded there. When restricting the analysis to 272 European species already naturalized outside of Europe, the naturalization debt decreased but remained relatively high with values in the range 81-100% (mean = 96%) with the former threshold and 52-100% (95%) with the latter threshold.

The proportion of observed naturalizations that are correctly predicted based on environmental matching (sensitivity) ranged from 0 to 100% for all thresholds and both species sets. However, the average value of sensitivity was two percentage points lower for the full set of species (19-64%) than for the subset of already naturalized species (21-66%). The average proportion of unsuccessful naturalizations in unsuitable environments (negative predictive value) was between 98.8% and 100% (mean = 99.9%) with the lowest threshold, and between 97.0% and 100% (mean = 99.7%) with the highest threshold for the full set of species. When considering already naturalized species only, the negative predictive value decreased substantially to the range 80.0-100% (mean = 99.4%) in the former case and 83.4-100% (mean = 98.8%) in the latter case. The threshold of 1% of suitable cells offered the best solution for maximizing sensitivity while still having a high negative predictive value when comparing observed and expected naturalized floras. Therefore, we used predictions from this threshold in the subsequent analyses.

Naturalization debt was lower in more developed regions (human development index > 0.7) (Figures 3 and 4) with moist and cool climates, including coastal North America, Japan, temperate Australia and New Zealand (Figure 5). Sensitivity increased progressively with the level of development and inventory effort (Figures 3 and 4), and reached maximum values in North-East America, the South American Atlantic Forest and the southern Andes, Turkey, the East-Central African mountains, South Africa, Japan, temperate Australia and New Zealand (Figure 5). The negative predictive value was lower in more developed regions (human development index > 0.7), with more treaties relevant to biological invasions (number of treaties > 20; Figures 3 and 4), including regions in North America, the southern tip of South

America and Africa, most of northern Asia excluding Mongolia, temperate Australia and New Zealand (Figure 5).

Plant features explaining naturalization patterns

Compared to plant species that are currently not known to be naturalized somewhere else (1,213), those that are naturalized (272) tend to be more widespread in Europe, to have a wider expected range outside Europe, and to have an ornamental or other economic use (Figure 6). There was no significant difference in functional traits between naturalized and non-naturalized species.

On average, species were found to be naturalized in 4.2% of their potentially suitable regions outside Europe (Figure S4). Thirty of the species occupied less than 0.1% of suitable regions and 31 species occupied more than 10% of suitable regions. The species with the most complete range filling was *Syringa vulgaris* (Oleaceae), native to the Balkan Peninsula and Romania, being currently naturalized in 70% of its suitable regions (Table S2). The average range expansion into regions estimated to be unsuitable was 0.4%. 118 species (43%) exhibited range expansion above 0.1%, but only one species had a range expansion above 10%: *Verbascum virgatum* (Scrophulariaceae), native to south-western Europe and southern England, and currently naturalized in 10.5% of the regions that were predicted to be unsuitable for it. We found that species performing best at filling their expected range have an ornamental or other economic relevance, a higher SLA, and a narrower expected range than species with a less complete range filling (Table 2). Furthermore, species observed as naturalized beyond their expected range tend to have an ornamental or other economic use and to be less widespread in their native range than species with no range expansion (Table 2).

Discussion

The global geographic pattern of richness in naturalized plant species from Europe is non-random as supported by our results, originating from a complex interplay of at least four mechanisms: 1) environmental matching between the native range of individual species and their expected alien range, which largely controls unsuccessful naturalization; 2) the alteration of the environment in the alien ranges by socio-economic activities (after accounting for sampling effort); 3) introduction pressure associated with the economic use of the species; and 4) differences in functional traits (e.g., SLA), which cause some species to more completely fill their expected alien ranges than others.

Accounting for environmental matching to decipher patterns of naturalization

We modelled environmental tolerance of species and then the influence of extrinsic socio-economic drivers (Figure 1), instead of both together as done in previous studies (Essl *et al.*, 2015; Dawson *et al.*, 2017). This allowed us to separate the effect of environmental matching in explaining the global pattern of richness in naturalized plant species from Europe. We elucidated that the environment alone is able to correctly predict up to two thirds of successful naturalizations (i.e., sensitivity) and 99.9% of unsuccessful naturalizations (i.e., negative predictive value), depending on the method used to compare local expected distributions with regional observed distributions (‘upscaling method’; Figure 2). Based on a similar approach, Bellard *et al.* (2013) showed that even the so-called “world's 100 worst invasive alien species” have a quite restricted expected range, covering mainly Europe and the areas along the Atlantic coast of North America. Thus, it clearly appears that knowing the available suitable environmental space of species is critical to assess the factors that determine their naturalization success.

Our approach indicated that non-European regions are currently occupied by less than 5% of the endemic European plants for which the area, or parts of it, would be suitable (Figure 2). Therefore, all regions have an enormous naturalization debt. This debt suggests that many endemic European plants have not been introduced outside of Europe yet or that they still have not overcome the biotic barriers provided by herbivores, pathogens and native competitors or the lack of important mutualists. Nevertheless, the large environmentally suitable ranges outside of Europe confirm that European plants have a considerable potential of naturalization outside their native range (van Kleunen *et al.*, 2015; Pyšek *et al.*, 2017), once they have overcome dispersal barriers and biotic resistance. Our results therefore indicate that it is unlikely that the number of new naturalizations will soon have reached its peak.

SDMs are increasingly used as a basis to implement biosecurity policies, e.g., by drawing up watch lists or lists of undesirable species (e.g., Padayachee *et al.*, 2019). As biosecurity measures are usually taken at a regional scale while SDMs predict expected distributions at smaller scales, it is critical to determine which portion of a region should be suitable for an alien species to become naturalized, and hence, of concern. Our retrospective approach comparing SDM outputs with the current naturalized flora from Europe in 931 non-European regions showed that a threshold in the order of 1% of a focal region offers a good trade-off between maximizing correctly predicted successful and unsuccessful naturalizations (Figure 2). Nevertheless, it may be preferable to choose a lower threshold with the precautionary principle, and this threshold might change when using a different spatial resolution.

Socio-economic drivers explaining differences from expected patterns of naturalization

Our results revealed that naturalization debt mostly decreases with the level of development (Figures 3 and 4), which means that a higher proportion of species with the ability to become naturalized are observed as such in more developed regions. In these regions, the distribution of naturalized species is typically closer to an equilibrium with the environment. This result is in line with Pyšek *et al.* (2010) and Dawson *et al.* (2017), who found that human impact (represented by proxies like wealth and per capita GDP, respectively) play a leading role in driving the global patterns of animal and plant naturalizations. One explanation is that economic wealth is often associated with alien species introductions and with profound alteration of natural habitats, which benefit alien species establishment and growth (MacDougall & Turkington, 2005; Seebens *et al.*, 2015).

Surprisingly, unlike other studies (Dawson *et al.*, 2017; Tingley *et al.*, 2018), proxies of international transport (i.e., density of airports and seaports in our study) did not explain naturalization debt (Figures 3 and 4). Nevertheless, we found that regions with the lowest naturalization debt are all either coastal or island regions (coastal North America, Algeria, Japan, temperate Australia and New Zealand; Figure 5). As a result, although naturalization debt seems little influenced by the density of seaports, it is likely that the volume of maritime traffic, or at least the presence of seaports, does play a significant role by increasing the rates of species introductions. One might argue that this pattern also reflects that coastal regions are usually more strongly developed than more inland regions as a consequence of the increasing demand for infrastructures to sustain residential, commercial and tourist activities (Figure S2), which offers more opportunities for introduction and naturalization of alien plants in coastal regions (Gallardo *et al.*, 2015). We found that naturalization debt was higher for the full set of 1,485 European species (either already naturalized or not yet naturalized) than for the subset of 272 species already naturalized, which are more likely to have overcome dispersal barriers (Figure 2). This suggests that introduction pathways influence naturalization debt although, unfortunately, it remains difficult to assess by how much.

In addition to the influence of development and potentially of introduction pathways on naturalized range filling, sensitivity was also found to be affected by the magnitude of inventory effort (Figures 3 and 4). Specifically, regions with the highest quality record of native plant richness also tend to have more records of alien plants. This is also corroborated by Dawson *et al.* (2017), and indicates that the geographic coverage of reported plant naturalizations remains unevenly exhaustive across regions so that our findings might be significantly influenced by biases in recording effort. In contrast, the negative predictive value decreased in regions with more treaties relevant to invasive alien species (Figures 3 and 4). This most likely does not indicate that treaties promote invasions, but that it is more likely that a region adopts a treaty when it has many invasive species. The effectiveness of these relatively recent treaties in preventing new invasions can only be assessed in the future.

Unexpectedly, human population density and the proportion of cropland had a relatively low contribution in explaining the global pattern of naturalization. Contrary to this, high human population densities are thought to influence the likelihood of an introduced species becoming naturalized and spreading through human impacts on the environment (Essl *et al.*, 2011; Pyšek *et al.*, 2010). Similarly, intensive agriculture (associated with historical sowing or planting of now naturalized species and associated weed-seed contaminants) is largely recognized to be a major cause of new introductions of naturalized and invasive species (Bellard *et al.*, 2016; Perrings *et al.*, 2005; Seebens *et al.*, 2015). A potential explanation for the low contributions of population density and the proportion of cropland in driving patterns of naturalization could be its redundancy with the proportion of primary land cover used as environmental variable in SDMs since urbanization and agriculture are largely responsible for land conversion (Chini *et al.*, 2014). Although this redundancy makes it difficult to isolate the effect of human population density and agriculture, we believe the introduction of primary land cover in SDMs was critical in this study to distinguish plants that are drivers and passengers of human-induced disturbances (MacDougall & Turkington, 2005). Another possible cause for the low contribution of agriculture is the ancient human colonization history of Europeans who used to transport cultivated plants across continents while other regions only recently opened up to international movements of plants (di Castri, 1989). In this perspective, most of the plants used in agriculture and associated weeds endemic to Europe with the potential to become naturalized might have already largely spread worldwide (Monnet *et al.*, 2020).

Plant features explaining differences from expected patterns of naturalization

The average score of alien geographic range filling of naturalized plants from Europe was 4.2%. This might appear to be very low compared to percentages of environmental niche filling reported in other studies (Hill *et al.*, 2017; Petitpierre *et al.*, 2012; Strubbe *et al.*, 2013, 2015; Liu *et al.*, 2020). However, it should be noted that it is easier to fill a niche than to fill all locations that have that niche. None of our species had a range filling above the commonly used threshold of 90%. Similarly, no invasive birds showed more than 90% of their native niche filled in the invasive range (Strubbe *et al.*, 2013). However, no less than 52% of invasive plants (Petitpierre *et al.*, 2012), 32% of 22 insects (Hill *et al.*, 2017) and 10% of vertebrates (Strubbe *et al.*, 2015) had a niche filling above 90%. Moreover, only one naturalized plant species from Europe out of 272 had a range expansion above the commonly used threshold of 10%, while it was the case for the niche expansion of 55% of invasive insects (Hill *et al.*, 2017), 29% of birds (Strubbe *et al.*, 2013), 17% of vertebrates (Strubbe *et al.*, 2015) and 14% of invasive plants (Petitpierre *et al.*, 2012).

We found that SLA was positively correlated with range filling of naturalized plants from Europe (Table 2). According to the LHS scheme of Westoby (1998), SLA is a proxy for rapid growth and an acquisitive resource-use strategy, which would be typical of resource-rich and/or disturbed environments, both of which have become more common in the last centuries due to human activities. In the competitor/stress-tolerator/ruderal (CSR) framework of the universal adaptive strategy theory (Grime, 1977), rapid growth is a key characteristic of strong competitors, suggesting that strong competitors for light and nutrients are also filling their naturalized ranges faster. Indeed, Guo *et al.* (2018) recently showed that species with high scores on the competitor axis were more likely to naturalize. Thus, it seems very consistent that having a high SLA represents a key strategy in regions subject to intensive development associated with rapid, deep and widespread anthropogenic perturbations. SLA should therefore also indicate potential for faster expansion towards the equilibrium range in alien regions. This corroborates previous results showing that SLA is higher for naturalized and invasive species compared to non-naturalized or native species (van Kleunen *et al.*, 2010; Pyšek & Richardson, 2007; Pyšek *et al.*, 2015).

Interestingly, seed mass was not significantly related to range filling (Table 2). This trait can have contrasting effects on patterns of naturalization since large seeds have greater nutrient reserves, which increases the chances to become naturalized, but small seeds are beneficial for long-distance dispersal and therefore favour spread (Crawley *et al.,* 1996; Moodley *et al.*, 2013). This suggests that it is not a species' dispersal ability or the ability to settle in new regions that mainly drive naturalization but the ability to be transported by humans for aesthetic or economic values. Our results showed that species used by humans are indeed more frequently naturalized (Figure 6), and perform better at filling (e.g., *Syringa vulgaris*) and expanding (e.g., *Verbascum virgatum*) their potential range than species not used by humans (Table 2). Ornamental horticulture, agriculture and forestry are recognized as major pathways of alien plant introduction. For instance, it has been estimated that at least 75% and 93%, respectively, of the naturalized alien plants worldwide are grown in domestic and botanical gardens (van Kleunen *et al.*, 2018), and plants with a known economic importance are 18 times more likely to be naturalized somewhere in the world (van Kleunen *et al.*, 2020). Possible reasons include: economic importance increases the number of releases and/or the number of individuals released (i.e., propagule pressure), while human selection favours traits related to invasiveness (e.g., ease to grow and reproduce, early and long flowering period, low susceptibility to insect pests or pathogens).

Moreover, we found that the same set of distributional features explains whether or not species are naturalized and the extent of naturalized range filling and geographic expansion of species range (range filling and expansion were significantly correlated; $r = 0.61$, P-value < 0.001), but in opposite directions. Indeed, naturalized species tend to be more widespread in their native range and to have wider expected alien ranges than non-naturalized species, i.e., they are typically generalist species (Gallien *et al.*, 2019). In contrast, naturalized species with the most complete range filling and broadest range extension tend to have more limited expected alien ranges and to be less widespread in their native range, respectively. This result needs to be interpreted with caution since it can simply arise from a numerical artefact as it may be easier to fill a small expected range than a large one. Another possible cause could be that SDMs tend to be more accurate for specialist species than for generalists (Connor *et al.*, 2018). Furthermore, range filling depends on opportunities to disperse, so species with a wider expected alien range may basically have less chance to fill it. Finally, more narrowly distributed endemics can surprisingly have a greater range expansion if their observed distribution in the native range results from biogeographical (e.g., the Mediterranean Basin, the Alps in Europe) or from biological interactions rather than from climatic barriers. In that case SDMs would fail to fit their fundamental climatic envelope due to niche truncation (Bush *et al.*, 2018). It could also be that their current distribution is matching their climatic niche, but that this distribution is not correctly reflected in data sources, maybe because they mostly inhabit under-sampled regions. Consequently, the projected expected alien ranges may underestimate the true potential ranges.

Conclusions

Our findings indicate that the environment largely controls the expected naturalized range of European plants. We demonstrated that increased anthropogenic disturbance associated with human development as well as increased probability of introductions associated with international exchange primarily explain the extent to which species spread within their expected naturalized range. We showed that plants selected for ornamental and other economic purposes perform better at filling and expanding their range, most likely because of increased introduction pressure and a preference for cultivating plants with traits that also make them more likely to naturalize. We revealed that species with functional traits indicative of rapid growth and acquisitive resource use tend to fill their range more completely than species with slower responses. These findings give a new overall picture of the drivers of naturalization that can help plan future studies on the macroecology of alien species as well as in designing future biosecurity plans. As harmful invasive species emerge from the pool of naturalized species, the analysis of which species could naturalize is a first step in identifying species that could ultimately become invasive in a region.

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Table 1 Summary of the seven socio-economic factors used to assess the drivers of naturalization success of the European vascular plants including the year and spatial resolution at which the original data was collected/calculated, the range of values for the regions used in analyses, and which transformation was applied to these values prior to analyses. Minimum and maximum values are those, after transformation, over the 526 non-European regions for which all socio-economic factors were available.

Variable	Year	Resolution	Unit	Min	Max	Transformation
Introduction pathways						
Airports	2019	-	100,000 km^{-2}	0	11	log
Seaports	2014	-	100,000 km^{-2}	0	15	log
Treaties	2016	-	#	6	30	-
Human pressures						
Population	2000	1 km	Inhabitant.km^{-2}	0	10	log
Cropland	< 2007	5 arcmin	%	0	95	-
Development	2015	5 arcmin	Dimensionless	.27	.93	-
Sampling effort						
Inventory	2015-16	110 km	%	0	249	-

Table 2 Regression coefficients of the relationship between distributional, economic and functional features of naturalized plants from Europe and their range filling (proportion of suitable regions where species are observed as naturalized) and range expansion (proportion of unsuitable regions where species are observed as naturalized). Continuous variables were standardized to allow comparison. Significance levels of the relationships fitted with linear mixed-effect models accounting for between-species phylogenetic distances are indicated by asterisks (.05 < *P*-value ≤ .01: *; .01 < *P*-value ≤ .001: **, *P*- value < .001: ***).

	Range filling	Range expansion	*n*
Prevalence in Europe	0.13	**-0.40***	272
Potential range outside Europe	**-0.25****	0.08	272
Ornamental	**0.22*****	**0.14***	272
Other use	**0.21*****	**0.22*****	272
Growth form	0.02	0.01	193
Specific leaf area (SLA)	**0.27***	-0.01	117
Height	0.05	0.01	175
Seed mass	0.02	-0.01	156

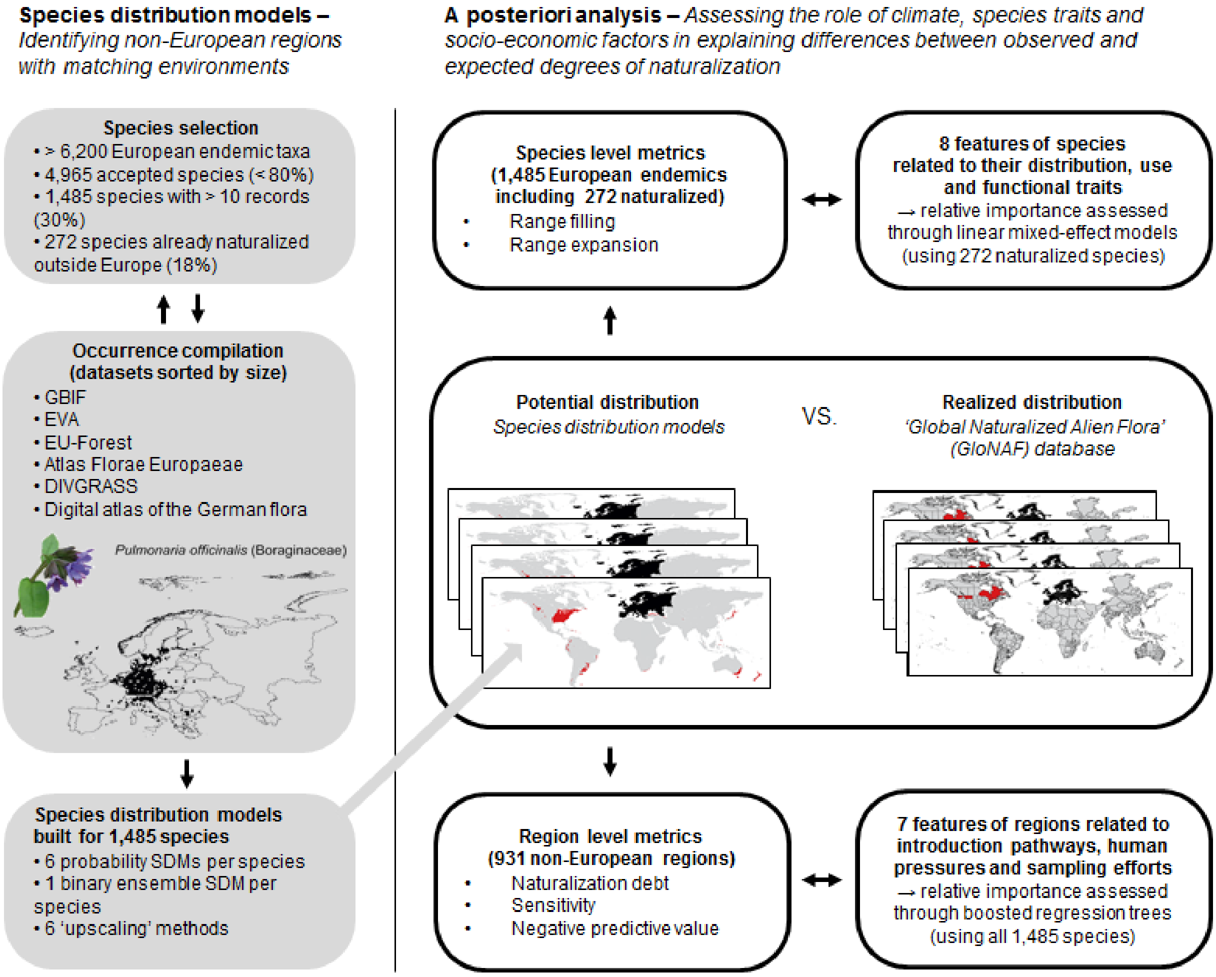

Figure 1 Workflow of this study used to determine which features of both plants and recipient regions explain possible discrepancies between observed and expected extents of naturalization.

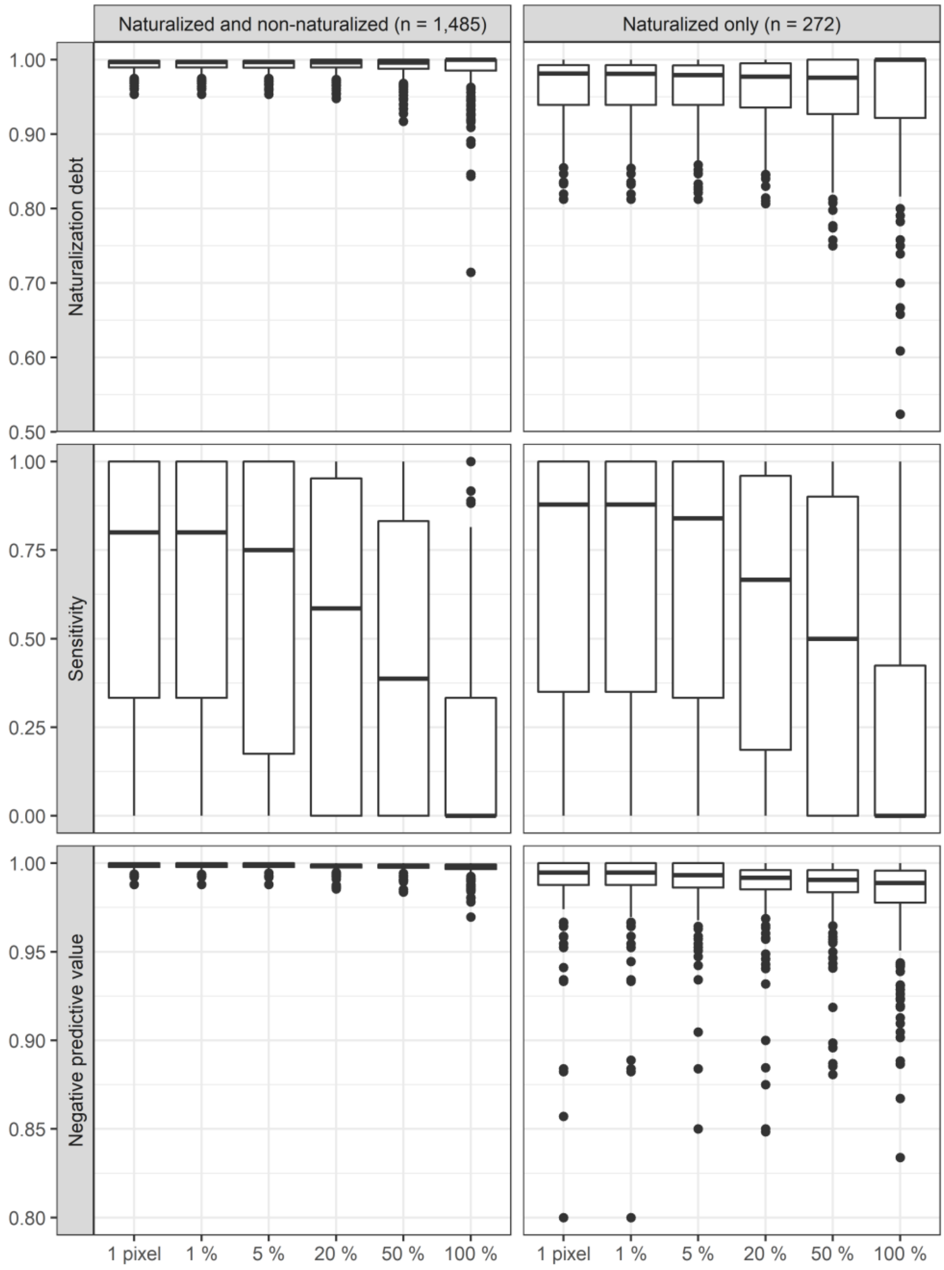

Figure 2 Comparison of predicted and observed naturalized floras in 931 non-European regions based on various upscaling methods used to transform local naturalization predictions into regional naturalization predictions. The left column comprises our full set of European plants (either already naturalized or not yet naturalized outside of Europe) and the right column comprises only the subset of those plants already naturalized outside of Europe. Naturalization debt refers to the proportion of predicted naturalizations that are not yet observed, sensitivity to the proportion of correctly predicted successful naturalizations and

negative predictive value to the proportion of correctly predicted unsuccessful naturalizations. A region was considered suitable if it contained at least one suitable pixel, 1% suitable cells, 5%, 20%, 50%, and 100%.

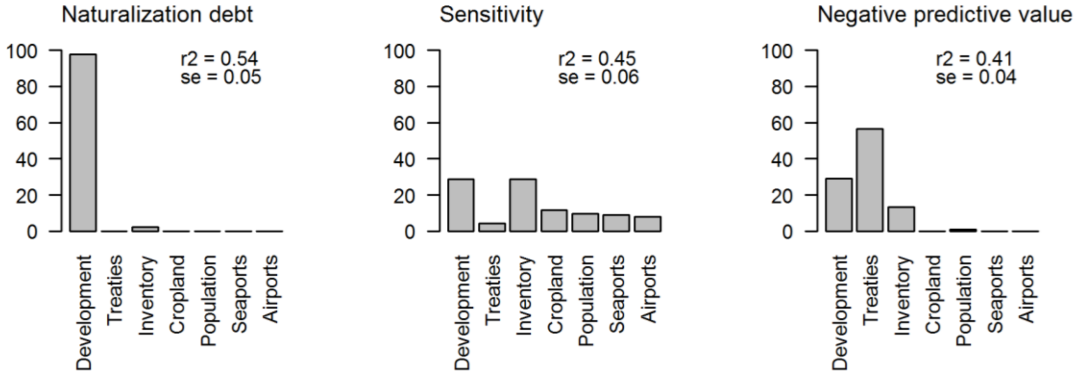

Figure 3 Relative influence of seven socio-economic factors in explaining differences between observed and expected European naturalized floras calculated by boosted regression trees. Naturalization debt refers to the proportion of predicted naturalizations that are not yet observed, sensitivity to the proportion of correctly predicted successful naturalizations and negative predictive value to the proportion of correctly predicted unsuccessful naturalizations. Socio-economic factors are sorted by mean relative influence over the three metrics. These results are for the upscaling method ‘1 %’ i.e., a region was considered suitable for a species if it contained at least 1% suitable cells.

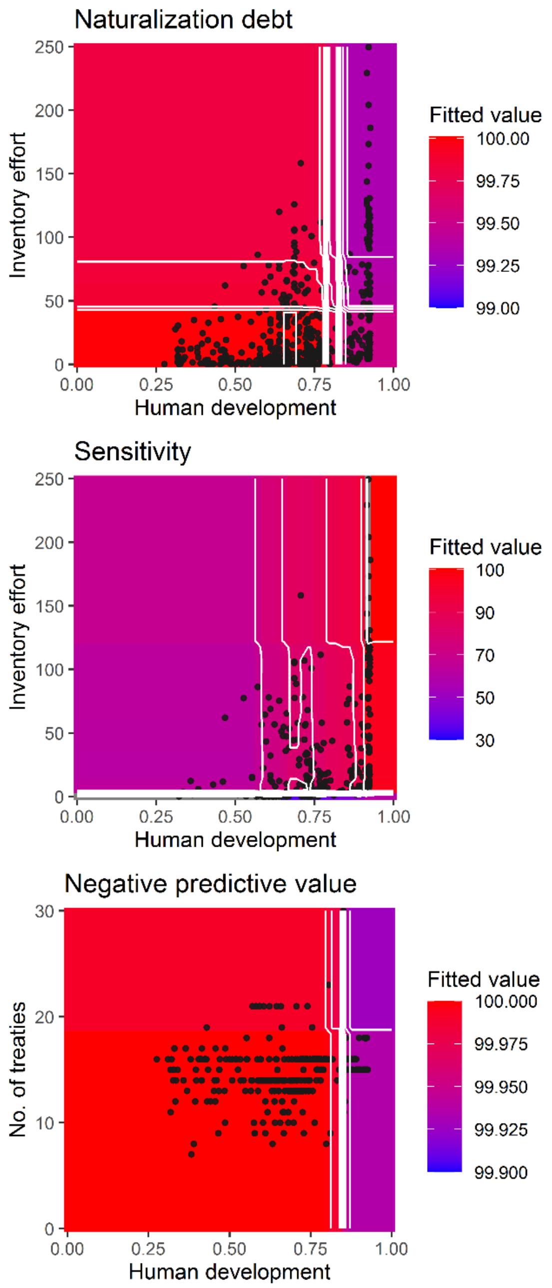

Figure 4 Joint partial dependence plots of interactions fitted by boosted regression trees between the most contributing regional socio-economic factors and differences between observed and expected European naturalized floras. Naturalization debt refers to the proportion of predicted naturalizations that are not yet observed, sensitivity to the proportion of correctly predicted successful naturalizations and negative predictive value to the proportion of correctly predicted unsuccessful naturalizations. Black dots represent empirical data points. These results are for the upscaling method ‘1 %’ i.e., a region was considered suitable for a species if it contained at least 1% suitable cells.

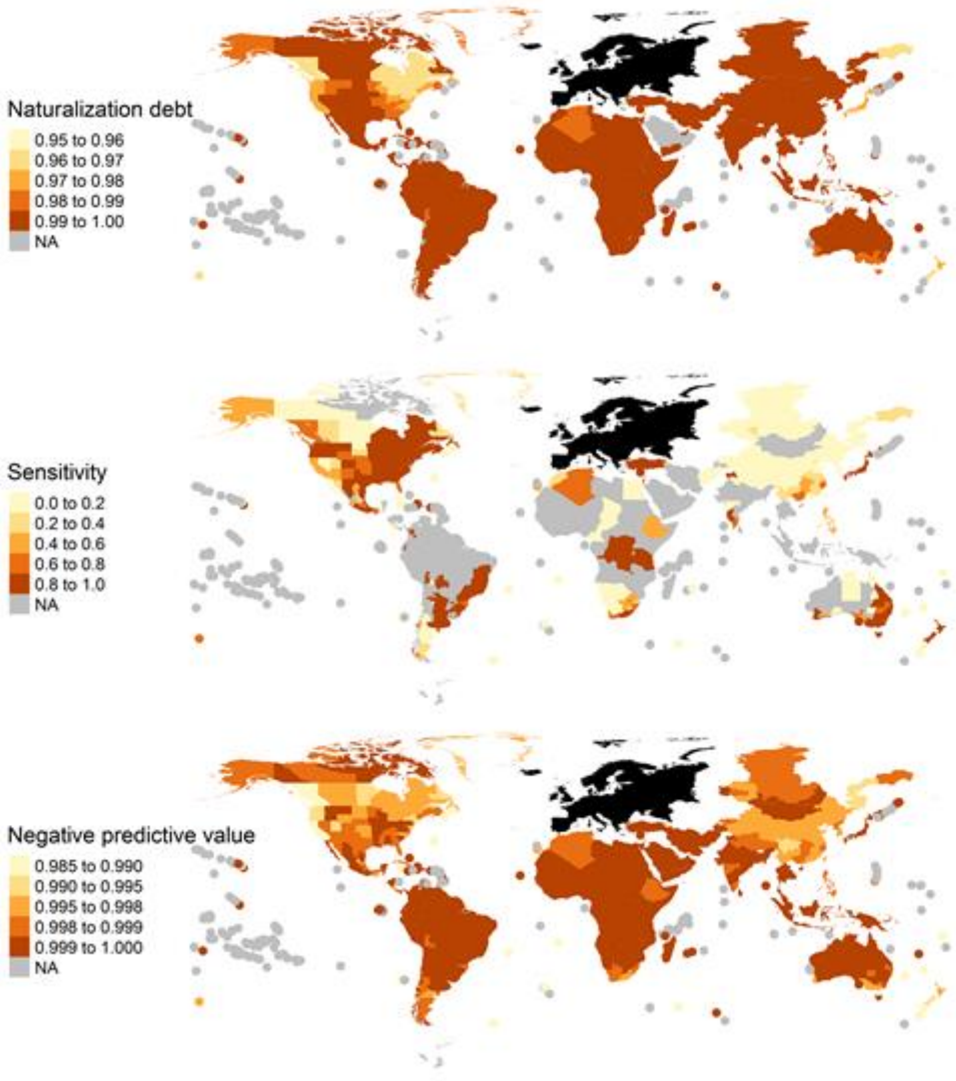

Figure 5 Global maps of the differences between observed and expected European naturalized floras. Regions with no GloNAF data are displayed in white. Naturalization debt refers to the proportion of predicted naturalizations that are not yet observed, sensitivity to the proportion of correctly predicted successful naturalizations (there are many NA values as many regions have no observed naturalizations by European endemic plants) and negative predictive value to the proportion of correctly predicted unsuccessful naturalizations. These results are for the upscaling method '1 %' i.e., a region was considered suitable for a species if it contained at least 1% suitable cells.

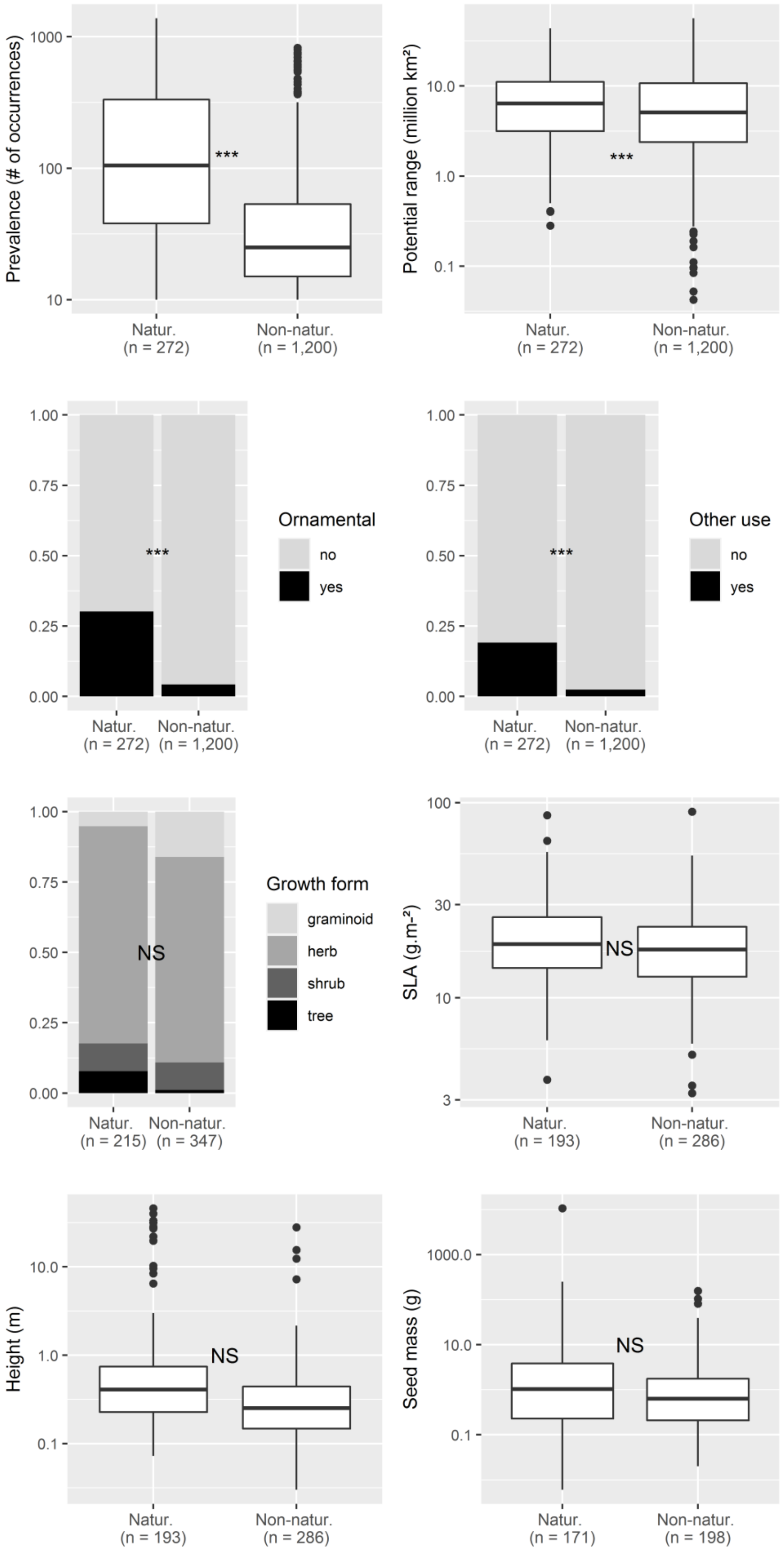
Prevalence (# of occurrences)
1000
100
10
***
Natur.
(n = 272)
Non-natur.
(n = 1,200)
Potential range (million km²)
10.0
1.0
0.1
***
Natur.
(n = 272)
Non-natur.
(n = 1,200)
1.00
0.75
0.50
0.25
0.00
***
Ornamental
no
yes
Natur.
(n = 272)
Non-natur.
(n = 1,200)
1.00
0.75
0.50
0.25
0.00
***
Other use
no
yes
Natur.
(n = 272)
Non-natur.
(n = 1,200)
1.00
0.75
0.50
0.25
0.00
NS
Growth form
graminoid
herb
shrub
tree
Natur.
(n = 215)
Non-natur.
(n = 347)
SLA (g.m⁻²)
100
30
10
3
NS
Natur.
(n = 193)
Non-natur.
(n = 286)
Height (m)
10.0
1.0
0.1
NS
Natur.
(n = 193)
Non-natur.
(n = 286)
Seed mass (g)
1000.0
10.0
0.1
NS
Natur.
(n = 171)
Non-natur.
(n = 198)

Figure 6 Difference in distributional, economic and functional features between European vascular plants already recorded as naturalized outside Europe (‘Natur.’) and those not recorded as naturalized outside Europe (‘Non-natur.’), 1,472 species in total. ‘Prevalence’ refers to the number of 0.42° × 0.42° cells in Europe occupied, ‘Potential range’ to the surface area of the species’ expected range outside Europe, ‘Ornamental’ and ‘Other use’ indicate whether species are used as an ornamental plant or has other economic relevance (e.g., food plant, medicines, materials), respectively, ‘Growth form’ reflects the morphology of a plant, especially its physiological adaptation to the environment, ‘SLA’ for ‘specific leaf area’ is the ratio of leaf area to leaf dry mass, ‘Height’ and ‘Seed mass’ are the plant height and seed mass. Significance levels of the relationships fitted with linear mixed-effect models accounting for between-species phylogenetic distances are indicated by asterisks (.05 < *P*-value ≤ .01: *; .01 < *P*-value ≤ .001: **, *P*-value < .001: ***).