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

Robin Pouteau, Wilfried Thuiller, Carsten Hobohm, Caroline Brunel, Barry J. Conn, Wayne Dawson, Michele de Sá Dechoum, Aleksandr L. Ebel, Franz Essl, Ori Fragman-Sapir, et al.

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1 **Research paper**

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

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## 269 **Data availability statement**

270 The data used to build the species distribution models (occurrence records and  
271 environmental variables) came from openly accessible repositories cited in the manuscript  
272 (for details on the EVA database, see <http://euroveg.org/eva-database-obtaining-data>). All  
273 1,485 generated habitat suitability raster files are available at  
274 <https://dataverse.ird.fr/dataset.xhtml?persistentId=doi:10.23708/RNGS8Z>.

275 **Research paper**

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

278 **Running title:** Observed versus expected naturalizations

279 **Abstract**

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

286 *Location* – Global.

287 *Time period* – Present.

288 *Major taxa studied* – Vascular plants.

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

297 *Results* – In terms of suitable area, **more than 95%** of expected naturalizations of European  
298 plants were not yet observed. Species were naturalized in only 4.2% of their suitable regions

299 outside of Europe (range filling) and in 0.4% of their unsuitable regions (range expansion).  
300 Anthropogenic habitat disturbance primarily explained the difference between observed and  
301 expected naturalized European floras, as did the number of treaties relevant to invasive  
302 species. Species of ornamental and economic value and with large specific leaf area  
303 performed better at filling and expanding beyond their expected range.

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

308

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

## 312 **Introduction**

313 Species that maintain self-sustaining populations outside their native range independently of  
314 direct human intervention (i.e., naturalized species; Richardson *et al.*, 2000; Blackburn *et al.*,  
315 2011) pose a serious concern to native biodiversity and ecosystem functioning and services  
316 worldwide (IPBES, 2019). Their number has increased substantially over the last few  
317 centuries and does not show any indication of saturation (Seebens *et al.*, 2017). Regions  
318 differ considerably in their richness of naturalized species of vascular plants, and species  
319 vary considerably in their extent of naturalization (Pyšek *et al.*, 2017, Essl *et al.*, 2019). Part  
320 of this variation may result from regional differences in the size of the potential naturalized  
321 alien pool and the size of the range potentially available for naturalized species. Little is  
322 known about the relationship of the observed and potential richness of naturalized plant  
323 species (i.e. the maximum numbers of alien species that these regions could host given  
324 species' environmental tolerances; Stohlgren *et al.*, 2008).

325 The actual distribution of naturalized alien plant species results from [the number of](#)  
326 [introductions by humans \(intentional or not\) followed by](#) the interplay of factors that  
327 determine the environmental space available for a species and factors that prevent or  
328 promote the extent to which an equilibrium with an environmental space is reached.  
329 Environmental suitability (e.g., climate, habitat) determines the potential (expected)  
330 distribution range by filtering the subset of introduced species that can maintain populations  
331 over long periods by successfully reproducing, i.e., naturalized species (Richardson & Pyšek,  
332 2012). Human activities can further influence the observed distribution range of species by  
333 altering environmental conditions and dispersal processes that dictate opportunities for  
334 introductions. For instance, human transport, trade and increasing urban development tend  
335 to broaden observed ranges, while, conversely, biosecurity responses can contain this  
336 expansion (Hulme, 2009).



337 An increasing body of literature is investigating what proportions of species' potential alien  
338 ranges are actually occupied (Petitpierre *et al.*, 2012; Strubbe *et al.*, 2013, 2015; Hill *et al.*,  
339 2017; Liu *et al.*, 2020). Indeed, most alien species are occupying only a subset of the niche  
340 corresponding to suitable environments that are occupied in their native range ('niche filling').  
341 Certain alien species are also able to colonize new environments that are not occupied in  
342 their native range ('niche expansion'). Patterns of niche filling and niche expansion vary  
343 highly depending on the type of organisms. For instance, the average niche filling was found  
344 to be 80% for vascular plants considered invasive (i.e., spreading into areas away from sites  
345 of introduction; Richardson *et al.*, 2000), 37% for invasive insects and 20% for invasive birds,  
346 whereas the average niche expansion was 26% for birds, 20% for insects and 5% for plants  
347 (Petitpierre *et al.*, 2012; Strubbe *et al.*, 2013; Hill *et al.*, 2017). Niche changes during  
348 invasions appear to be primarily driven by introduction history (e.g., propagule pressure and  
349 colonization processes) in birds, and by human disturbance in insects (Hill *et al.*, 2017).  
350 However, little is known about what causes possible differences between observed and  
351 expected ranges in naturalized plants.

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

363 naturalized species should be an important step in understanding the influence of socio-  
364 economic factors on observed patterns of naturalization (Xu *et al.*, 2019).

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

378 Europe is the second-most important donor continent of naturalized alien plant species, after  
379 Asia. However, the European flora is by far the most successful in naturalizing. Of the  
380 ~14,200 vascular plant species [native \(i.e. both endemic and non-endemic\)](#) to Europe, 3,383  
381 have become naturalized somewhere in the world; this is three times more than expected by  
382 chance (van Kleunen *et al.*, 2015). Furthermore, five of the 10 globally most widely  
383 naturalized species are native to Europe (Pyšek *et al.*, 2017). The European flora is therefore  
384 suitable for studying drivers of differences between observed and expected naturalized  
385 ranges.

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

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

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

## 406 **Materials and methods**

### 407 *Expected naturalized ranges*

#### 408 Species selection

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

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

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

#### 426 Compilation of species occurrence records

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

434 When several occurrence records from these different sources were duplicated on the same  
435 cell, only one occurrence record per species was kept to avoid pseudoreplication. Cell size  
436 was set to  $0.42^\circ \times 0.42^\circ$  (~50 km  $\times$  50 km at the equator) to approach the resolution of the  
437 source of occurrence records having the coarsest resolution (Atlas Florae Europaeae). Using  
438 a higher resolution (i.e., a smaller cell size) would have required to downscale this source of  
439 occurrence records, which typically introduces spatial biases and uncertainty in the model  
440 predictions (Bonbi & D'Amen, 2012). Moreover, this resolution appeared to be a good

441 compromise to account for the fact that the selected environmental variables (climate, land  
442 use and soil type) determine invasion potential at different scales (10,000 to 200 km, 2,000 to  
443 10 km, and 10 km to 10 m, respectively; Milbau *et al.*, 2009).

444 Species with fewer than 10 deduplicated occurrence records were not further considered  
445 since the resulting SDM might be inaccurate. The final dataset comprised 135,189  
446 occurrence records for a total of 1,485 European plant species, belonging to 327 genera and  
447 67 families (Table S1), i.e. on average 91 occurrence records per species with a maximum of  
448 1,382 occurrence records for *Achillea ptarmica* (Asteraceae). We had enough occurrence  
449 records to build an SDM (i.e., 10 occurrences) for 272 European species among the 407  
450 already naturalized species and for 1,213 species currently not known to be naturalized  
451 anywhere.

#### 452 Environmental predictors of expected ranges

453 We defined six environmental variables to model and project species expected ranges.  
454 These variables were related to climate, land use, and soil physico-chemical properties,  
455 which are commonly recognized to shape the distribution of plants (Gurevitch *et al.*, 2006).  
456 Annual mean temperature (°C), annual precipitation (mm) and precipitation seasonality  
457 (yearly coefficient of variation) representing the period 1979-2013 were provided at a 30  
458 arcsec resolution by the CHELSA climate database (Karger *et al.*, 2017). Worldwide  
459 correlations between these variables and the others described below did not exceed the  
460 threshold of  $|r| = 0.70$  (Supporting Information Appendix Figure S1) beyond which collinearity  
461 begins to severely distort model estimations and subsequent predictions (Dormann *et al.*,  
462 2013). However, these variables reflecting trends in average climate conditions were  
463 significantly correlated with climate extremes to which plants are recognized to be highly  
464 responsive (Zimmermann *et al.*, 2009). The percentage of each grid cell with primary land  
465 cover based on the Harmonized Global Land Use models was also used (Chini *et al.*, 2014).  
466 Organic carbon content (g per kg) and pH in the first 15 cm of soil were extracted at a 1 km

467 resolution from the global gridded soil information database SoilGrids (Hengl *et al.*, 2014).  
468 Environmental variables were aggregated (using the mean value) to the resolution of 0.42° ×  
469 0.42°.

#### 470 Species distribution modelling

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

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

493 1 indicating a perfect fit, an AUC of 0.5 meaning that predictions from SDM do not differ from  
494 random, and an AUC of 0 meaning the SDM is always incorrect. TSS ranges from -1 to 1,  
495 where 1 indicates perfect agreement and 0 indicates a random prediction.

496 To combine the predictive capability of the six SDMs, their projections were subsequently  
497 aggregated into an average or consensus projection. To ensure the quality of the ensemble  
498 SDM, we only kept the projections for which the accuracy estimated by AUC and TSS were  
499 higher than 0.8 and 0.6, respectively, and assembled the selected SDMs using a committee-  
500 average approach with each SDM was weighted proportional to its TSS evaluation.

501 Probability maps obtained from the ensemble forecasting projections were then transformed  
502 into binary suitable/non-suitable maps using the threshold maximizing the TSS to ensure the  
503 most accurate predictions, since it is based on both sensitivity and specificity. The entire  
504 species distribution modelling workflow was performed within the 'biomod2' R platform  
505 (Thuiller *et al.*, 2009).

#### 506 *Recorded naturalized ranges*

507 The current observed naturalized range of the European flora was obtained through the  
508 GloNAF database version 1.2, a recently compiled database of ~14,000 naturalized alien  
509 plant species covering 1,029 regions worldwide, corresponding to administrative regions  
510 such as countries, states and provinces, and also including 381 islands (van Kleunen *et al.*,  
511 2019). The size of a region ranged from 0.03 km<sup>2</sup> (Tauna islet of the Gambier archipelago,  
512 French Polynesia) to 2,486,952 km<sup>2</sup> (the Republic of the Sudan plus South Sudan). A total of  
513 407 European [endemic](#) species were found as naturalized in at least one of the non-  
514 European GloNAF regions.

515 We explored various definitions of suitability by analyzing what proportion of a region should  
516 be suitable for a species to become naturalized in this region. The following definitions were  
517 used: at least one suitable cell, 1%, 5%, 20%, 50%, or 100% suitable cells, respectively. For  
518 each region, species were classified into: true positives (TP), i.e., species that are both

519 observed and predicted as being successfully naturalized in the region; false positives (FP),  
520 i.e., species that have not become naturalized, but are predicted as successfully naturalized;  
521 false negatives (FN), i.e., species that are observed as successfully naturalized but not  
522 predicted to be naturalized; and true negatives (TN), i.e., species that are neither predicted  
523 nor observed to be naturalized in the region. Then, the predicted naturalized species pool  
524 was compared to the observed naturalized pool by calculating: 1) the naturalization debt in  
525 the broad sense hereafter referred to as 'naturalization debt' ( $FP/(TP+FP)$ ), i.e., the  
526 proportion of predicted naturalizations that are not yet observed either because species are  
527 not yet introduced to the focal area (introduction debt) or because they were introduced, but  
528 are not naturalized yet (naturalization debt in the strict sense, i.e., *sensu Rouget et al., 2016*),  
529 which can take several decades or centuries for some taxa; 2) the assemblage sensitivity  
530 ( $TP/(TP+FN)$ ), i.e., the proportion of observed naturalizations that are correctly predicted ; 3)  
531 the negative predictive value ( $TN/(TN+FN)$ ), i.e., the proportion of species that were not  
532 predicted to be naturalized and have not become naturalized in the region.

### 533 *Socio-economic drivers of naturalization patterns*

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



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

### 555 *Plant features explaining naturalization patterns*

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

573 height–seed (LHS) scheme of Westoby (1998). Correlation between LHS traits was  $|r| <$   
574 0.27. Functional traits were extracted from the TRY database (Kattge *et al.*, 2020). Linear  
575 mixed-effect models (LMMs) were fitted using a phylogenetic generalized least square  
576 approach (PGLS) to compare features of naturalized and non-naturalized species while  
577 controlling for between-species phylogenetic distances (for details on the phylogeny used,  
578 see Appendix S4). As we did not have data on all features for each species (see Figure 6),  
579 we ran separate LMMs for each of the eight features. LMMs were performed using the *gls()*  
580 function of the R package ‘nlme’ (Pinheiro *et al.*, 2019).

581 We used LMMs accounting for phylogeny to test whether plant-feature values explain: 1) the  
582 relative extent of range filling, i.e., the proportion of suitable regions where a species has  
583 become naturalized; and 2) the relative extent of range expansion, i.e., the proportion of  
584 unsuitable regions where a species has nevertheless become naturalized. The indices of  
585 range filling and expansion that we used are similar to the indices used by Petitpierre *et al.*  
586 (2012). However, we calculated them in the geographical space instead of in the  
587 environmental space because occurrence data on naturalized plants are not evenly  
588 comprehensive across regions (which would have been needed to offer a reliable fit of the  
589 niches), and when an alien species is reported, we do not always know whether or not it  
590 reproduces in the wild (Figure 1).

## 591 **Results**

### 592 *Socio-economic drivers of naturalization patterns*

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

599 29% of species for which a region is suitable according to the lowest and highest thresholds,  
600 respectively, have actually been recorded there. When restricting the analysis to 272  
601 European species already naturalized outside of Europe, the naturalization debt decreased  
602 but remained relatively high with values in the range 81-100% (mean = 96%) with the former  
603 threshold and 52-100% (95%) with the latter threshold.

604 The proportion of observed naturalizations that are correctly predicted based on  
605 environmental matching (sensitivity) ranged from 0 to 100% for all thresholds and both  
606 species sets. However, the average value of sensitivity was two percentage points lower for  
607 the full set of species (19-64%) than for the subset of already naturalized species (21-66%).  
608 The average proportion of unsuccessful naturalizations in unsuitable environments (negative  
609 predictive value) was between 98.8% and 100% (mean = 99.9%) with the lowest threshold,  
610 and between 97.0% and 100% (mean = 99.7%) with the highest threshold for the full set of  
611 species. When considering already naturalized species only, the negative predictive value  
612 decreased substantially to the range 80.0-100% (mean = 99.4%) in the former case and  
613 83.4-100% (mean = 98.8%) in the latter case. The threshold of 1% of suitable cells offered  
614 the best solution for maximizing sensitivity while still having a high negative predictive value  
615 when comparing observed and expected naturalized floras. Therefore, we used predictions  
616 from this threshold in the subsequent analyses.

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

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

### 628 *Plant features explaining naturalization patterns*

629 Compared to plant species that are currently not known to be naturalized somewhere else  
630 (1,213), those that are naturalized (272) tend to be more widespread in Europe, to have a  
631 wider expected range outside Europe, and to have an ornamental or other economic use  
632 (Figure 6). There was no significant difference in functional traits between naturalized and  
633 non-naturalized species.

634 On average, species were found to be naturalized in 4.2% of their potentially suitable regions  
635 outside Europe (Figure S4). Thirty of the species occupied less than 0.1% of suitable regions  
636 and 31 species occupied more than 10% of suitable regions. The species with the most  
637 complete range filling was *Syringa vulgaris* (Oleaceae), native to the Balkan Peninsula and  
638 Romania, being currently naturalized in 70% of its suitable regions (Table S2). The average  
639 range expansion into regions estimated to be unsuitable was 0.4%. 118 species (43%)  
640 exhibited range expansion above 0.1%, but only one species had a range expansion above  
641 10%: *Verbascum virgatum* (Scrophulariaceae), native to south-western Europe and southern  
642 England, and currently naturalized in 10.5% of the regions that were predicted to be  
643 unsuitable for it. We found that species performing best at filling their expected range have  
644 an ornamental or other economic relevance, a higher SLA, and a narrower expected range  
645 than species with a less complete range filling (Table 2). Furthermore, species observed as  
646 naturalized beyond their expected range tend to have an ornamental or other economic use  
647 and to be less widespread in their native range than species with no range expansion (Table  
648 2).

### 649 **Discussion**

650 The global geographic pattern of richness in naturalized plant species [from Europe](#) is non-  
651 random as supported by our results, originating from a complex interplay of at least four

652 mechanisms: 1) environmental matching between the native range of individual species and  
653 their expected alien range, which largely controls unsuccessful naturalization; 2) the  
654 alteration of the environment in the alien ranges by socio-economic activities (after  
655 accounting for sampling effort); 3) introduction pressure associated with the economic use of  
656 the species; and 4) differences in functional traits (e.g., SLA), which cause some species to  
657 more completely fill their expected alien ranges than others.

#### 658 *Accounting for environmental matching to decipher patterns of naturalization*

659 We modelled environmental tolerance of species and then the influence of extrinsic socio-  
660 economic drivers (Figure 1), instead of both together as done in previous studies (Essl *et al.*,  
661 2015; Dawson *et al.*, 2017). This allowed us to separate the effect of environmental matching  
662 in explaining the global pattern of richness in naturalized plant species [from Europe](#). We  
663 elucidated that the environment alone is able to correctly predict up to two thirds of  
664 successful naturalizations (i.e., sensitivity) and 99.9% of unsuccessful naturalizations (i.e.,  
665 negative predictive value), depending on the method used to compare local expected  
666 distributions with regional observed distributions ('upscaling method'; Figure 2). Based on a  
667 similar approach, Bellard *et al.* (2013) showed that even the so-called "world's 100 worst  
668 invasive alien species" have a quite restricted expected range, covering mainly Europe and  
669 the areas along the Atlantic coast of North America. Thus, it clearly appears that knowing the  
670 available suitable environmental space of species is critical to assess the factors that  
671 determine their naturalization success.

672 Our approach indicated that non-European regions are currently occupied [by less than 5%](#) of  
673 the endemic European plants for which the area, or parts of it, would be suitable (Figure 2).  
674 Therefore, all regions have an enormous naturalization debt. This debt suggests that many  
675 endemic European plants have not been introduced outside of Europe yet or that they still  
676 have not overcome the biotic barriers provided by herbivores, pathogens and native  
677 competitors or the lack of important mutualists. Nevertheless, the large environmentally

678 suitable ranges outside of Europe confirm that European plants have a considerable  
679 potential of naturalization outside their native range (van Kleunen *et al.*, 2015; Pyšek *et al.*,  
680 2017), once they have overcome dispersal barriers and biotic resistance. Our results  
681 therefore indicate that it is unlikely that the number of new naturalizations will soon have  
682 reached its peak.

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

### 693 *Socio-economic drivers explaining differences from expected patterns of naturalization*

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

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

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

732 Unexpectedly, human population density and the proportion of cropland had a relatively low  
733 contribution in explaining the global pattern of naturalization. Contrary to this, high human  
734 population densities are thought to influence the likelihood of an introduced species  
735 becoming naturalized and spreading through human impacts on the environment (Essl *et al.*,  
736 2011; Pyšek *et al.*, 2010). Similarly, intensive agriculture (associated with historical sowing or  
737 planting of now naturalized species and associated weed-seed contaminants) is largely  
738 recognized to be a major cause of new introductions of naturalized and invasive species  
739 (Bellard *et al.*, 2016; Perrings *et al.*, 2005; Seebens *et al.*, 2015). A potential explanation for  
740 the low contributions of population density and the proportion of cropland in driving patterns  
741 of naturalization could be its redundancy with the proportion of primary land cover used as  
742 environmental variable in SDMs since urbanization and agriculture are largely responsible for  
743 land conversion (Chini *et al.*, 2014). Although this redundancy makes it difficult to isolate the  
744 effect of human population density and agriculture, we believe the introduction of primary  
745 land cover in SDMs was critical in this study to distinguish plants that are drivers and  
746 passengers of human-induced disturbances (MacDougall & Turkington, 2005). Another  
747 possible cause for the low contribution of agriculture is the ancient human colonization  
748 history of Europeans who used to transport cultivated plants across continents while other  
749 regions only recently opened up to international movements of plants (di Castri, 1989). In this  
750 perspective, most of the plants used in agriculture and associated weeds endemic to Europe  
751 with the potential to become naturalized might have already largely spread worldwide  
752 (Monnet *et al.*, 2020).

### 753 *Plant features explaining differences from expected patterns of naturalization*

754 The average score of alien geographic range filling of naturalized plants from Europe was  
755 4.2%. This might appear to be very low compared to percentages of environmental niche  
756 filling reported in other studies (Hill *et al.*, 2017; Petitpierre *et al.*, 2012; Strubbe *et al.*, 2013,  
757 2015; Liu *et al.*, 2020). However, it should be noted that it is easier to fill a niche than to fill all  
758 locations that have that niche. None of our species had a range filling above the commonly



759 used threshold of 90%. Similarly, no invasive birds showed more than 90% of their native  
760 niche filled in the invasive range (Strubbe *et al.*, 2013). However, no less than 52% of  
761 invasive plants (Petitpierre *et al.*, 2012), 32% of 22 insects (Hill *et al.*, 2017) and 10% of  
762 vertebrates (Strubbe *et al.*, 2015) had a niche filling above 90%. Moreover, only one  
763 naturalized plant species from Europe out of 272 had a range expansion above the  
764 commonly used threshold of 10%, while it was the case for the niche expansion of 55% of  
765 invasive insects (Hill *et al.*, 2017), 29% of birds (Strubbe *et al.*, 2013), 17% of vertebrates  
766 (Strubbe *et al.*, 2015) and 14% of invasive plants (Petitpierre *et al.*, 2012).

767 We found that SLA was positively correlated with range filling of naturalized plants from  
768 Europe (Table 2). According to the LHS scheme of Westoby (1998), SLA is a proxy for rapid  
769 growth and an acquisitive resource-use strategy, which would be typical of resource-rich  
770 and/or disturbed environments, both of which have become more common in the last  
771 centuries due to human activities. In the competitor/stress-tolerator/ruderal (CSR) framework  
772 of the universal adaptive strategy theory (Grime, 1977), rapid growth is a key characteristic of  
773 strong competitors, suggesting that strong competitors for light and nutrients are also filling  
774 their naturalized ranges faster. Indeed, Guo *et al.* (2018) recently showed that species with  
775 high scores on the competitor axis were more likely to naturalize. Thus, it seems very  
776 consistent that having a high SLA represents a key strategy in regions subject to intensive  
777 development associated with rapid, deep and widespread anthropogenic perturbations. SLA  
778 should therefore also indicate potential for faster expansion towards the equilibrium range in  
779 alien regions. This corroborates previous results showing that SLA is higher for naturalized  
780 and invasive species compared to non-naturalized or native species (van Kleunen *et al.*,  
781 2010; Pyšek & Richardson, 2007; Pyšek *et al.*, 2015).

782 Interestingly, seed mass was not significantly related to range filling (Table 2). This trait can  
783 have contrasting effects on patterns of naturalization since large seeds have greater nutrient  
784 reserves, which increases the chances to become naturalized, but small seeds are beneficial  
785 for long-distance dispersal and therefore favour spread (Crawley *et al.*, 1996; Moodley *et al.*,

786 2013). This suggests that it is not a species' dispersal ability or the ability to settle in new  
787 regions that mainly drive naturalization but the ability to be transported by humans for  
788 aesthetic or economic values. Our results showed that species used by humans are indeed  
789 more frequently naturalized (Figure 6), and perform better at filling (e.g., *Syringa vulgaris*)  
790 and expanding (e.g., *Verbascum virgatum*) their potential range than species not used by  
791 humans (Table 2). Ornamental horticulture, agriculture and forestry are recognized as major  
792 pathways of alien plant introduction. For instance, it has been estimated that at least 75%  
793 and 93%, respectively, of the naturalized alien plants worldwide are grown in domestic and  
794 botanical gardens (van Kleunen *et al.*, 2018), and plants with a known economic importance  
795 are 18 times more likely to be naturalized somewhere in the world (van Kleunen *et al.*, 2020).  
796 Possible reasons include: economic importance increases the number of releases and/or the  
797 number of individuals released (i.e., propagule pressure), while human selection favours  
798 traits related to invasiveness (e.g., ease to grow and reproduce, early and long flowering  
799 period, low susceptibility to insect pests or pathogens).

800 Moreover, we found that the same set of distributional features explains whether or not  
801 species are naturalized and the extent of naturalized range filling and geographic expansion  
802 of species range (range filling and expansion were significantly correlated;  $r = 0.61$ ,  $P$ -value  
803  $< 0.001$ ), but in opposite directions. Indeed, naturalized species tend to be more widespread  
804 in their native range and to have wider expected alien ranges than non-naturalized species,  
805 i.e., they are typically generalist species (Gallien *et al.*, 2019). In contrast, naturalized  
806 species with the most complete range filling and broadest range extension tend to have more  
807 limited expected alien ranges and to be less widespread in their native range, respectively.

808 This result needs to be interpreted with caution since it can simply arise from a numerical  
809 artefact as it may be easier to fill a small expected range than a large one. Another possible  
810 cause could be that SDMs tend to be more accurate for specialist species than for  
811 generalists (Connor *et al.*, 2018). Furthermore, range filling depends on opportunities to  
812 disperse, so species with a wider expected alien range may basically have less chance to fill

813 it. Finally, more narrowly distributed endemics can surprisingly have a greater range  
814 expansion if their observed distribution in the native range results from biogeographical (e.g.,  
815 the Mediterranean Basin, the Alps in Europe) or from biological interactions rather than from  
816 climatic barriers. In that case SDMs would fail to fit their fundamental climatic envelope due  
817 to niche truncation (Bush *et al.*, 2018). It could also be that their current distribution is  
818 matching their climatic niche, but that this distribution is not correctly reflected in data  
819 sources, maybe because they mostly inhabit under-sampled regions. Consequently, the  
820 projected expected alien ranges may underestimate the true potential ranges.

## 821 **Conclusions**

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

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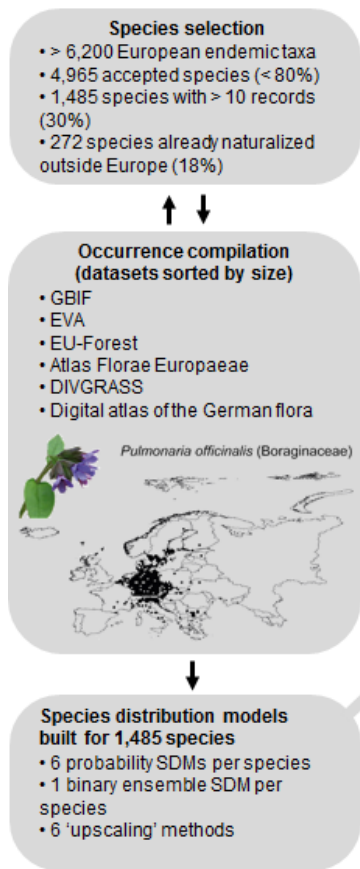
**Table 1** Summary of the seven socio-economic factors used to assess the drivers of naturalization success of the European vascular plants including the year and spatial resolution at which the original data was collected/calculated, the range of values for the regions used in analyses, and which transformation 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
<i>Introduction pathways</i>						
Airports	2019	-	100,000 km <sup>2</sup>	0	11	log
Seaports	2014	-	100,000 km <sup>2</sup>	0	15	log
Treaties	2016	-	#	6	30	-
<i>Human pressures</i>						
Population	2000	1 km	Inhabitant.km <sup>-2</sup>	0	10	log
Cropland	< 2007	5 arcmin	%	0	95	-
Development	2015	5 arcmin	Dimensionless	.27	.93	-
<i>Sampling effort</i>						
Inventory	2015-16	110 km	%	0	249	-

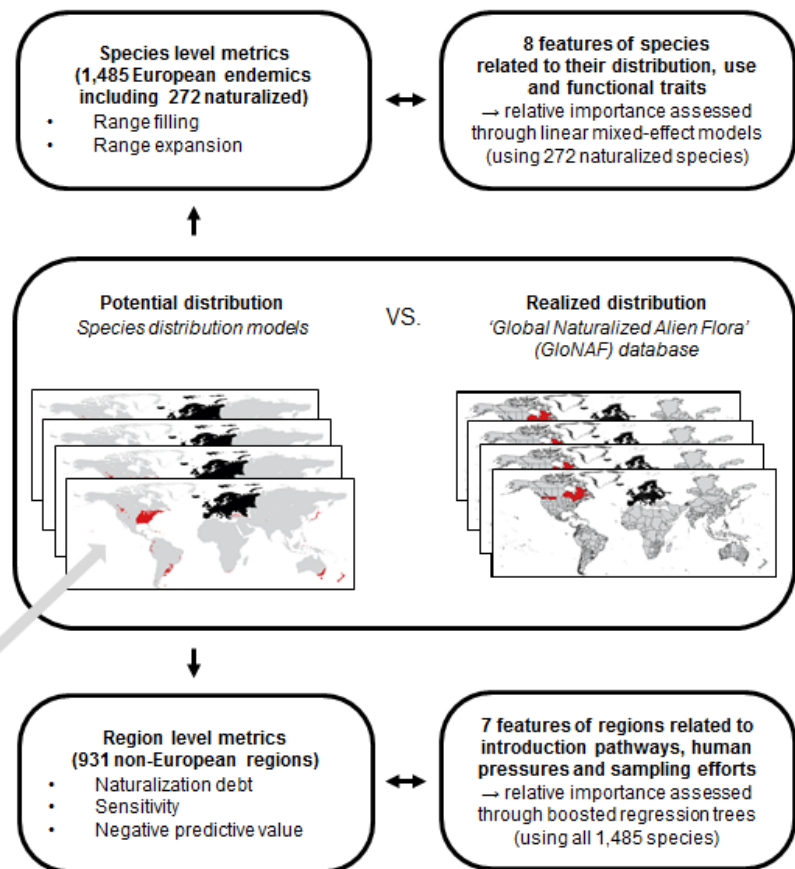
**Table 2** Regression coefficients of the relationship between distributional, economic and functional features of naturalized plants from Europe and their range filling (proportion of suitable regions where species are observed as naturalized) and range expansion (proportion of unsuitable regions where 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 ( $.05 < P\text{-value} \leq .01$ : \*,  $.01 < P\text{-value} \leq .001$ : \*\*,  $P\text{-value} < .001$ : \*\*\*).

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

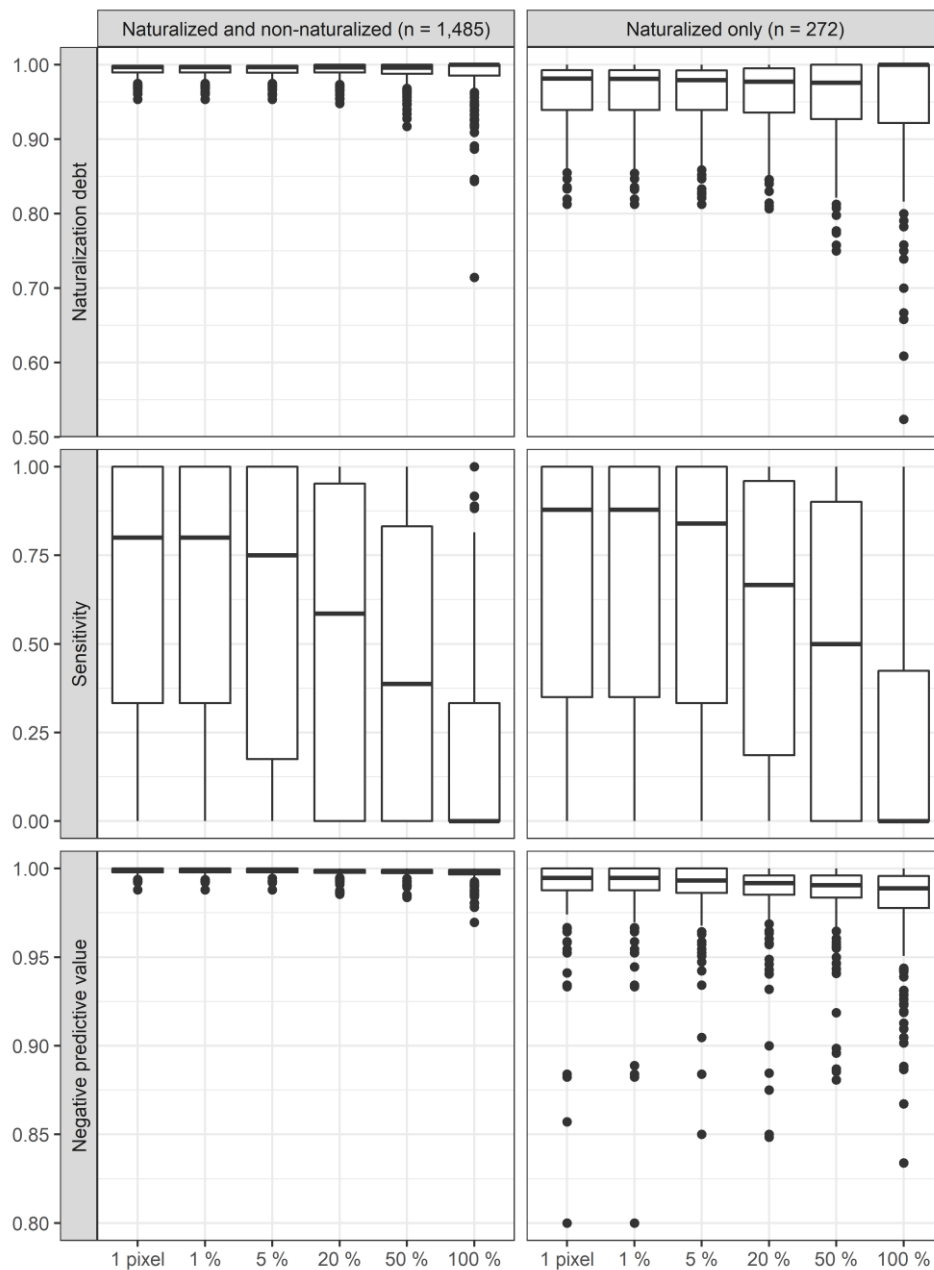
**Species distribution models – Identifying non-European regions with matching environments**



**A posteriori analysis – Assessing the role of climate, species traits and socio-economic factors in explaining differences between observed and expected degrees of naturalization**



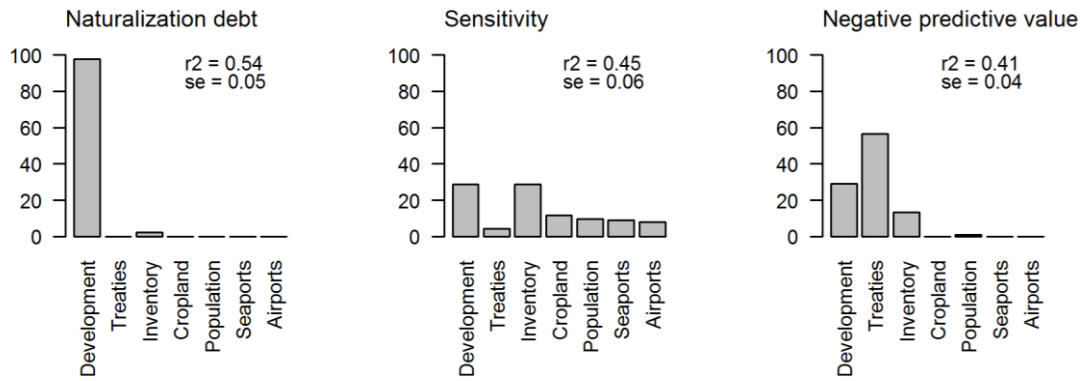
**Figure 1** Workflow of this study used to determine which features of both plants and recipient regions explain possible discrepancies between observed and expected extents of naturalization.



**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

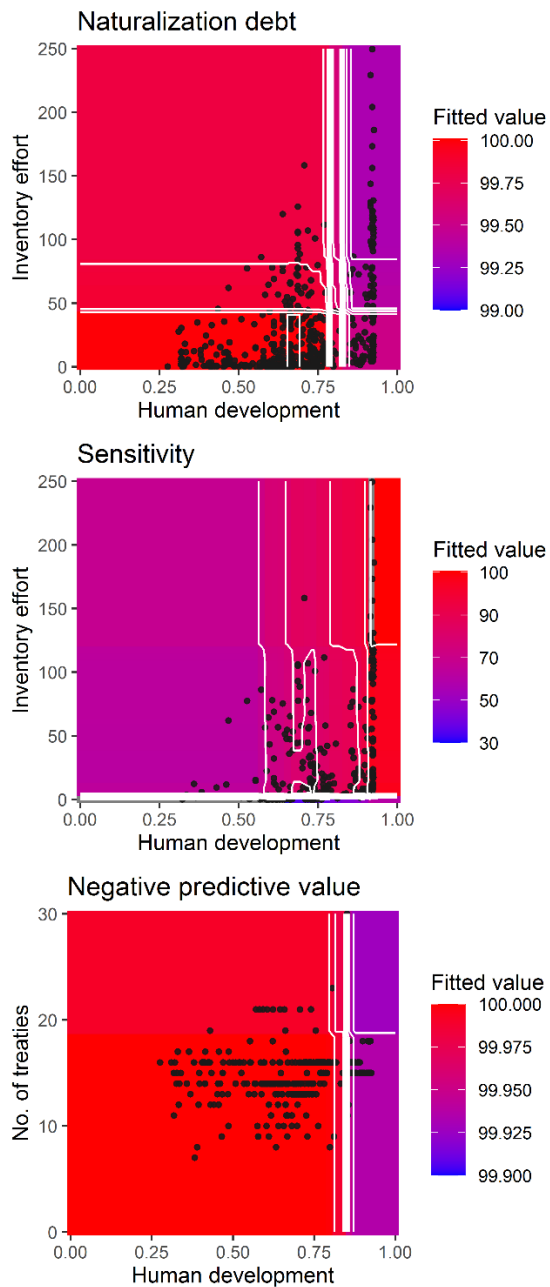
negative predictive value to the proportion of correctly predicted unsuccessful naturalizations.

A region was considered suitable if it contained at least one suitable pixel, 1% suitable cells, 5%, 20%, 50%, and 100%.

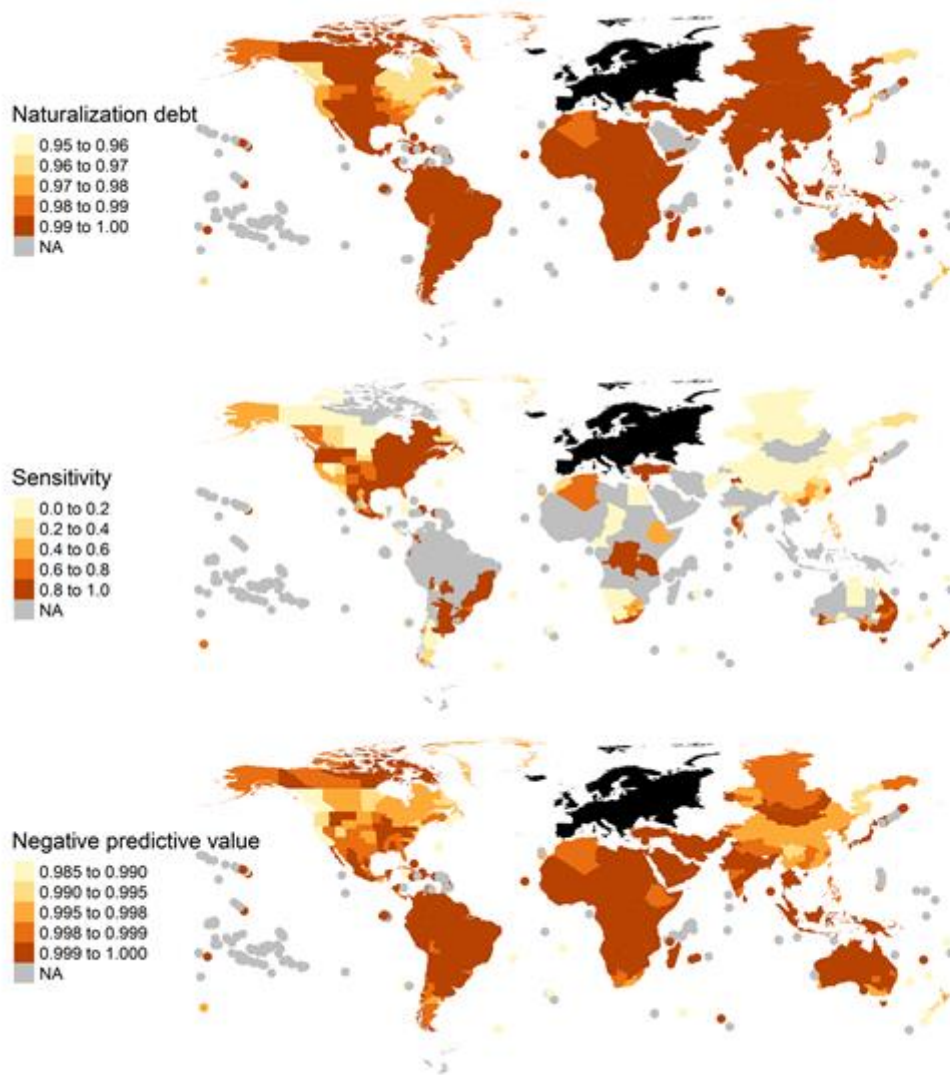


**Figure 3** Relative influence of seven socio-economic factors in explaining differences between observed and expected European naturalized floras calculated by boosted regression trees. Naturalization debt refers to the proportion of predicted naturalizations that are not yet observed, sensitivity 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.

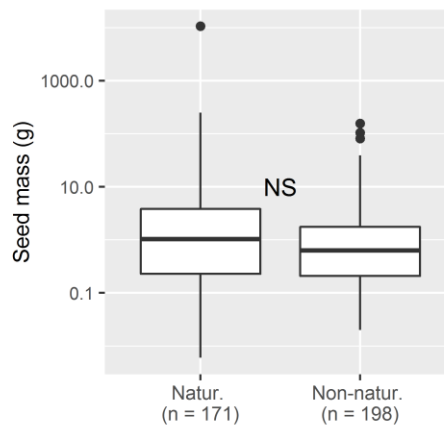
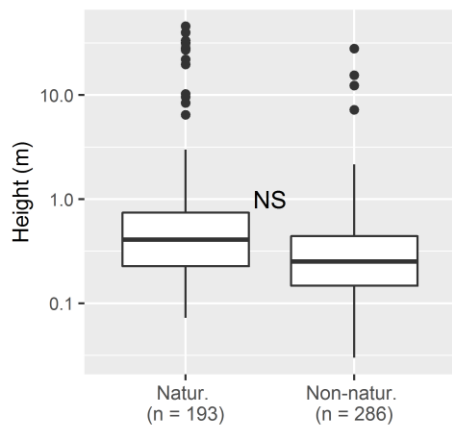
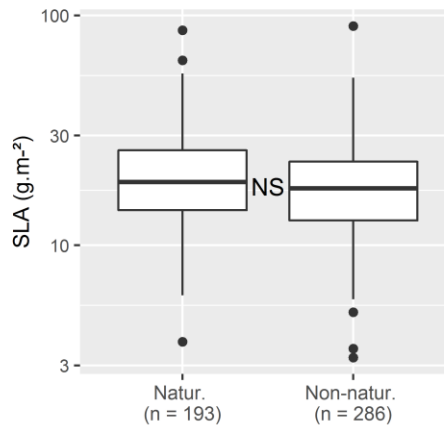
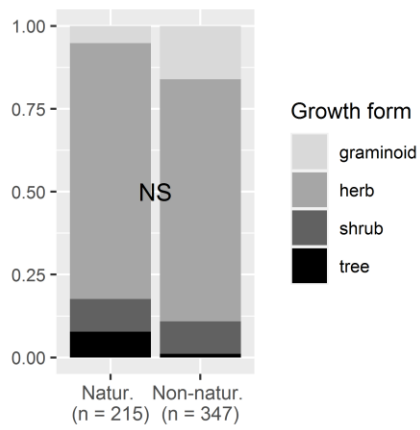
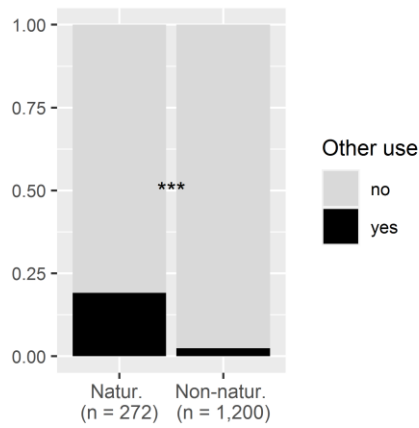
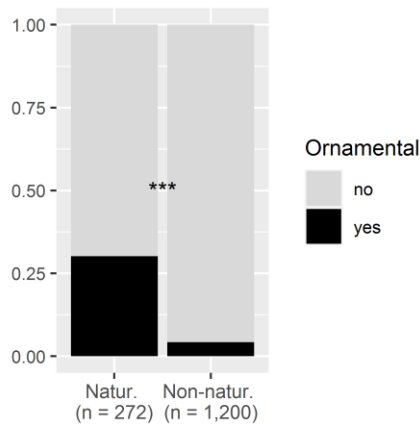
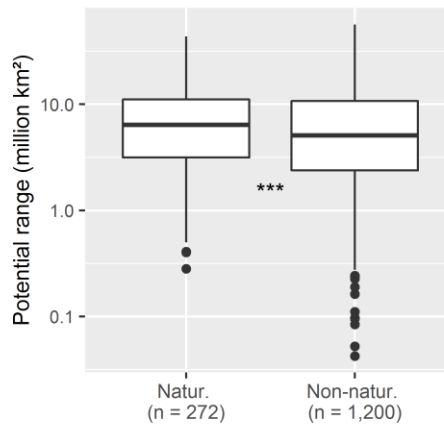
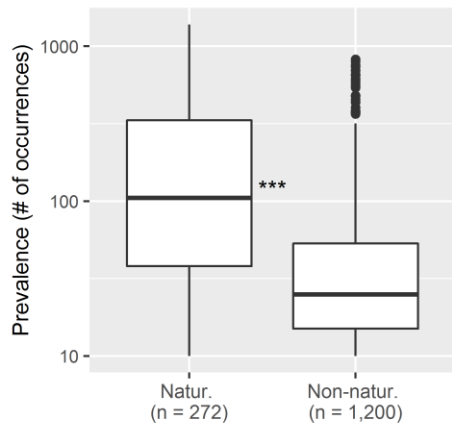




**Figure 4** Joint partial dependence plots of interactions fitted by boosted regression trees between the most contributing regional socio-economic factors and differences between observed and expected European naturalized floras. Naturalization debt refers to the proportion of predicted naturalizations 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.



**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  $0.42^\circ \times 0.42^\circ$  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 ( $.05 < P\text{-value} \leq .01$ : \*,  $.01 < P\text{-value} \leq .001$ : \*\*,  $P\text{-value} < .001$ : \*\*\*).