

European ornamental garden flora as an invasion debt under climate change

Emily Haeuser^{1,2}  | Wayne Dawson³  | Wilfried Thuiller⁴  | Stefan Dullinger⁵  |
Svenja Block⁶  | Oliver Bossdorf⁶  | Marta Carboni⁴  | Luisa Conti⁷  |
Iwona Dullinger^{5,8} | Franz Essl⁵  | Günther Klöner⁵  | Dietmar Moser⁵  |
Tamara Münkemüller⁴ | Madalin Parepa⁶ | Matthew V. Talluto⁴  | Holger Kreft⁹  |
Jan Pergl¹⁰  | Petr Pyšek^{10,11}  | Patrick Weigelt⁹  | Marten Winter¹²  | Martin
Hermy¹³  | Sebastiaan Van der Veken¹⁴ | Cristina Roquet⁴  | Mark van Kleunen^{2,15} 

¹Biology, San Diego State University, San Diego, California; ²Department of Biology, University of Konstanz, Konstanz, Germany; ³Conservation Ecology Group, Department of Biosciences, Durham University, Durham, UK; ⁴LECA-Laboratoire d'Ecologie Alpine, CNRS, Univ. Savoie Mont-Blanc, Univ. Grenoble Alpes, Grenoble, France; ⁵Botany and Biodiversity Research, Faculty of Life Sciences, University of Vienna, Vienna, Austria; ⁶Institute of Evolution & Ecology, University of Tübingen, Tübingen, Germany; ⁷Department of Botany, Faculty of Sciences, University of South Bohemia, České Budějovice, Czech Republic; ⁸Institute of Social Ecology, Faculty for Interdisciplinary Studies, Alps Adria University, Vienna, Austria; ⁹Biodiversity, Macroecology and Biogeography, University of Goettingen, Göttingen, Germany; ¹⁰Department of Invasion Ecology, Institute of Botany, The Czech Academy of Sciences, Průhonice, Czech Republic; ¹¹Department of Ecology, Faculty of Science, Charles University, Prague, Czech Republic; ¹²German Centre for Integrative Biodiversity Research, Halle-Jena-Leipzig, Leipzig, Germany; ¹³Division of Forest, Nature and Landscape, Department of Earth & Environmental Sciences, KU Leuven, Leuven, Belgium; ¹⁴Regionaal Landschap Kleine en Grote Nete, Kasterlee, Belgium and ¹⁵Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou, China

Correspondence

Emily Haeuser, Biology, San Diego State University, San Diego, CA.
Email: ehaeuser@sdsu.edu

Abstract

1. Most naturalised and invasive alien plant species were originally introduced to regions for horticultural purposes. However, many regions now face an invasion debt from ornamental alien species, which have not yet naturalised. In this regard, climate change represents a threat as it may lower the barriers to naturalisation for some ornamental alien species. Identifying those species is extremely important for anticipating impending invasions.
2. To identify predictors of naturalisation, we modelled the effects of climate, nursery availability and species characteristics on the current European naturalisation success of 2,073 ornamental aliens commonly planted in European gardens. We then used the resulting model together with climate projections for 2050 to forecast future naturalisation risks for the 1,583 species not yet naturalised in Europe.
3. We found that non-European naturalised range size, climatic suitability, propagule pressure, having a dioecious sexual system and plant height jointly explained current naturalisation success in Europe. By 2050, naturalisation probability projections increased by more than 0.1 for 41 species, and only decreased by more than 0.1 for one species.
4. *Policy implications.* Using predictions based on our integrated model of alien ornamental naturalisation success, we identified species with high future naturalisation risk and species with high projected increases in naturalisation potential in

Europe under climate change. This species list allows for prioritisation of monitoring and regulation of ornamental plants to mitigate the invasion debt.

KEYWORDS

biological invasions, climatic suitability, garden plants, invasion modelling, invasive plants, naturalisation success, propagule pressure, risk assessment

1 INTRODUCTION

Preventing alien species invasions is a global environmental priority (Secretariat of the Convention on Biological Diversity, 2000). Globally, already over 13,000 alien vascular plant species have established persistent wild populations outside of cultivation (Pyšek et al., 2017; van Kleunen et al., 2015). A subset of these so-called naturalised species (*sensu* Richardson et al., 2000) are known to have negative ecological impacts and are considered invasive (*sensu* Secretariat of the Convention on Biological Diversity, 2000). Most naturalised alien plants have originally been introduced intentionally from their native regions into other regions for cultivation in domestic or botanic gardens (van Kleunen et al., 2018). Given that globally, at least 170,000 plant species are in cultivation (van Kleunen et al., 2018), the garden flora constitutes an enormous pool of potential alien invaders (Pergl et al., 2016).

In Europe, c. 4,000 alien plant species are currently naturalised (Pyšek et al., 2017; van Kleunen et al., 2015), and the number is still increasing (Seebens et al., 2017). Preventing future naturalisations requires identifying species with naturalisation potential. One common strategy is to prevent introductions of species that are invasive elsewhere (e.g. Pheloung, Williams, & Halloy, 1999). This approach, however, ignores the risk posed by alien species that have already been introduced as garden plants but have not yet become naturalised. As there is often a time-lag between introduction and naturalisation (Essl et al., 2011; Kowarik, Pyšek, Prach, Rejmánek, & Wade, 1995), it is likely that some of the thousands of already introduced garden plants in Europe will naturalise and become invasive in the future.

Many ornamental species are being cultivated at latitudes higher than those of their natural distributions (Van der Veken, Hermy, Vellend, Knapen, & Verheyen, 2008), and their ability to naturalise is likely limited by suboptimal climate (but see Gallien et al., 2016). Ongoing climate change may lower this barrier for many alien ornamentals (Walther et al., 2009). These potential future invaders are considered to be an invasion debt (Essl et al., 2011). Through climate matching of the native and non-native ranges, it is possible to predict invasion success (Hayes & Barry, 2008). Using climatic suitability modelling, Dullinger et al. (2017) showed that the naturalisation risk from ornamental alien species will increase for much of Europe under projected future climates. Identifying the riskiest ornamental species is essential to prevent new naturalisations, and to assure that management resources are not wasted on species that pose less risk under future climatic conditions.

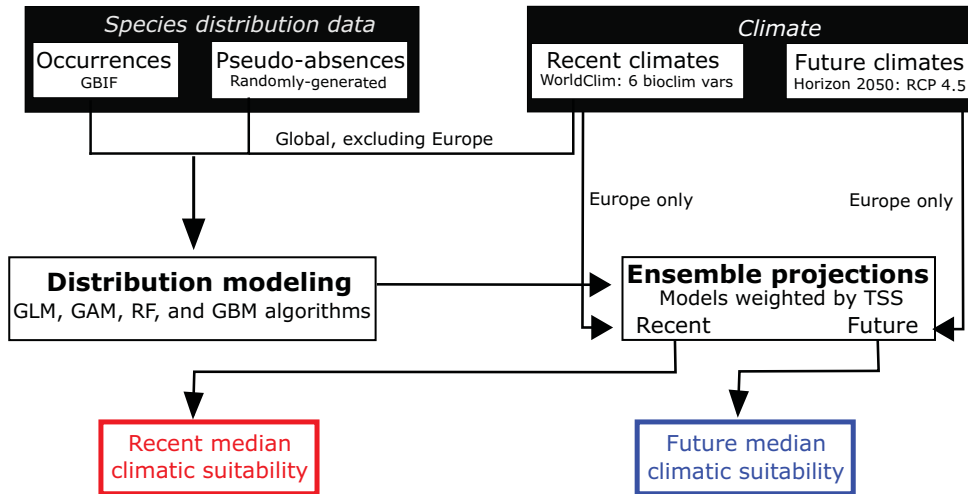
Several factors other than climatic suitability have been linked to naturalisation and need to be considered when assessing a species' naturalisation potential (Richardson & Pyšek, 2012). These include high propagule pressure (Dehnen-Schmutz, Touza, Perrings, & Williamson, 2007a; Kolar & Lodge, 2001; Lockwood, Cassey, & Blackburn, 2005), naturalisation success elsewhere (e.g. Kolar & Lodge, 2001; Mayer et al., 2017), native range size (Maurel, Hanspach, Kühn, Pyšek, & van Kleunen, 2016; Pyšek et al., 2009a, 2015; Razanajatovo et al., 2016) and certain species traits (Bucharová & van Kleunen, 2009; Hanspach, Kühn, Pyšek, Boos, & Klotz, 2008; Pyšek, Krivanek, & Jarošík, 2009b; Pyšek et al., 2009a, 2015; Razanajatovo et al., 2016; van Kleunen, Dawson, Schlaepfer, Jeschke, & Fischer, 2010). Moreover, the drivers of naturalisation success may interact (Küster, Kühn, Bruelheide, & Klotz, 2008). So far, few studies have examined how naturalisation success is influenced jointly by all of these factors and their interactions, and none have used this approach to forecast potential future naturalisations.

Here, we fill this gap by combining climatic suitability data with data on propagule pressure, naturalised range size outside of Europe, native range size, and several species traits (growth form, presence of storage organs, propagation method, sexual system, plant height and winter hardiness) to build a phylogenetically corrected model of European naturalisation success for 2,073 species of the European Garden Flora (Cullen, Knees, Cubey, & Shaw, 2012). Using suitability projections based on recent and projected future climates, we forecast future probability of naturalisation success for the 1,583 not-yet-naturalised ornamental alien species. This provides a list of species most likely to naturalise in Europe in the near future.

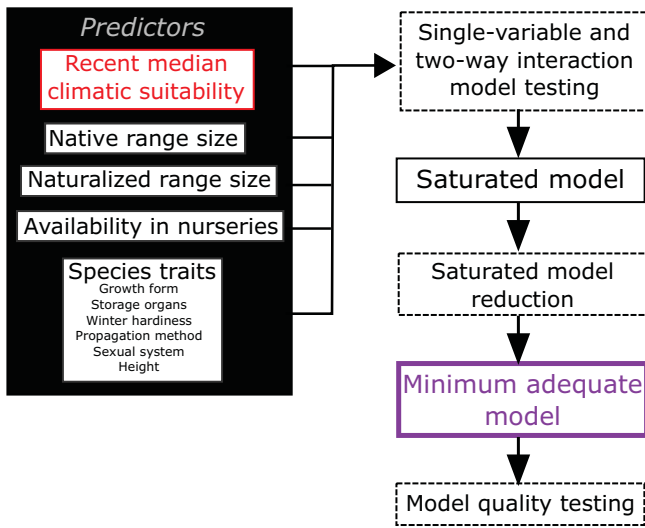
2 MATERIALS AND METHODS

We modelled recent naturalisation success and future naturalisation risk of 2,073 alien ornamental plants in Europe in three steps (Figure 1). (a) To estimate the recent and future climatic suitability for each species in Europe, we first modelled the link between recent climates and species presence outside of Europe and projected this onto Europe for the recent and future projected climates. (b) We then used recent climatic suitability in combination with other species characteristics to develop a minimal model explaining current naturalisation success of the species in Europe. (c) Finally, for the subset of species not yet naturalised in Europe, we parameterised the model with recent and projected future climatic suitability to

(a) Climatic suitability



(b) Naturalization success modeling



(c) Naturalization risk projections

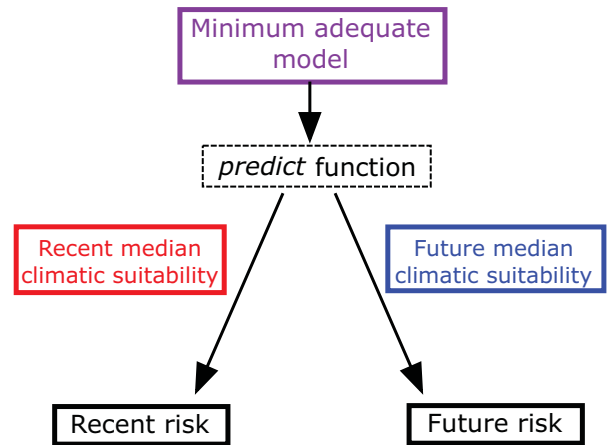


FIGURE 1 Workflow of analytical methods, including (a) climatic suitability modelling; (b) naturalisation success modelling; (c) recent and future naturalisation risk projections of non-naturalised alien species. Solid lines indicate objects (e.g. species characteristics, models, projections) and dashed lines indicate analytical methods (e.g. model reduction). Like colours indicate terms carried over between the three steps

assess the absolute future naturalisation risk and the change in naturalisation risk from that under recent climates.

We selected species from the European Garden Flora (EGF, Cullen et al., 2012), an encyclopaedia of >23,000 species and varieties commonly planted in European gardens, of which c. 13,500 are alien to Europe. As potential predictors of naturalisation success, we compiled data (see detailed descriptions below) on species' (a) native range, (b) naturalised range, (c) traits, (d) availability in nurseries and (e) climatic suitability. As these data came from numerous sources, we aligned all datasets after standardising species names using the *taxonstand* package version 1.8 (Cayuela & Oksanen, 2016) in R version 3.3.1 (R Core Team, 2017). Garden cultivars and subspecies were only considered at the species level. Complete data for all characteristics (except for native range size and minimum winter

temperature tolerances, see below) were available for 2,073 species alien to Europe.

2.1 Species characteristics

From the EGF (Cullen et al., 2012), we extracted information on the continents to which species are native. This allowed us to exclude all native EGF species from further analyses. As a proxy of species native range size, we used the number of Taxonomic Database Working Group (TDWG) level-2 regions (52 in total; Brummit, 2001) where a species is native. As sources for these data, we used the Germplasm Resources Information Network (GRIN; Wiersema, 1995) and Kew's World Checklist of Selected Plant Families (WCSP, 2017). We obtained native range-size data for 1,879 of the 2,073 species.

To determine naturalisation status of EGF species in Europe and as a proxy of naturalised range size outside of Europe, we used the Global Naturalized Alien Flora database (GloNAF version 1.1; van Kleunen et al., 2015; Pyšek et al., 2017). GloNAF provides naturalisation-status data for >13,000 species in 843 regions around the globe (covering 83% of the ice-free terrestrial land surface). Species listed as naturalised in any European GloNAF region were considered naturalised in Europe. For a proxy of naturalised range size outside of Europe, we extracted the number of non-European GloNAF regions where a species is listed as naturalised. We used number of regions rather than summed region area because species may not occupy entire regions, and because number of regions yielded better model fit (see detailed methods below).

From the EGF, we extracted several species characteristics: (a) growth form (woody: 44.7% of our species, herbaceous: 55.3%), (b) presence of storage organs (no: 68.8%, yes: 31.2%), (c) cultural propagation by seed (possible: 85.2%, not possible: 14.8%), (d) cultural propagation by vegetative cutting (possible: 82.6%, not possible: 17.4%), (e) sexual system (dioecious: 5.0%, non-dioecious [monoecious and hermaphroditic]: 95.0%), (f) maximum plant height and (g) winter hardiness (ranging from species tolerating minimum winter temperatures $\leq -20^{\circ}\text{C}$ to those only tolerating heated glasshouses). Except for winter hardiness, where data were available for 2,037 species, all other EGF species-characteristic data were available for all 2,073 species.

As a proxy of a species' propagule pressure, we tallied the number of European nurseries where it is available for sale ("availability in nurseries"). These data were compiled by Van der Veken et al. (2008) from sales catalogues of 237 European nurseries. Species' nursery availability ranged from 0 to 88 nurseries.

2.2 Climatic suitability projections

To assess each species' recent and potential future climatic suitability across the European continent (Figure 1a), we built for each species distribution models relating its occurrences outside of Europe to climatic conditions. We largely followed the methods of Dullinger et al. (2017) and Klöner et al. (2017), and a detailed description is provided in Appendix S1. In short, we combined species occurrence data from the Global Biodiversity Information Facility (GBIF, 2018 [<http://www.gbif.org>]) with six bioclimatic variables (averaged for the period 1950–2000) from WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005, www.worldclim.org), using the *biomod2* R package version 3.3-7 (Thuiller, Georges, & Engler, 2016). We used the WorldClim data rather than more recent alternatives (e.g. CHELSA, Karger et al., 2017), because it better reflects climatic conditions under which most of our species were introduced or naturalised. We then used these models to project a species' recent and future climatic suitability in Europe. For future European climatic suitability projections, we used climate-projection data for horizon 2050 under the moderate Representative Concentration Pathway (RCP) scenario 4.5. To get single integral recent and future climatic suitability values for

each species, we extracted the medians of the recent and future climatic suitability values across all European grid cells.

2.3 Modelling naturalisation success

In the next step (Figure 1b), we used the climatic suitability estimates together with the other species characteristics to model naturalisation success in Europe. To facilitate interpretation of the model estimates, continuous explanatory variables were centred to a mean of zero and scaled to a standard deviation of one (Schielzeth, 2010). For binary explanatory variables (i.e. growth form, storage-organ presence, propagation by seed, propagation by vegetative cutting and sexual system), the two levels of each variable were respectively assigned numeric values of 0 or 1. They were then also centred to a mean of zero, so that the model intercept corresponds to an average species (Schielzeth, 2010).

To account for possible effects due to phylogenetic non-independence of species, we used GenBank sequences to build a dated phylogenetic tree following Roquet, Thuiller, and Lavergne (2012). The tree was resolved at the genus level, and species were included as polytomies. We included phylogeny as a random variance structure in a generalised linear model (GLM) and assessed the effects of the different explanatory variables on species' current naturalisation status (yes, no) in Europe. The model was built using the R package *MCMCglmm* (Hadfield, 2010).

Because the large number of explanatory variables considered might result in over-fitting and convergence problems, we built a minimal adequate model following Feng et al. (2016). We first ran separate models incorporating each explanatory variable individually, and models for all possible pairwise combinations and interactions of explanatory variables. Because data were available for different numbers of species for some variables, we used in these models the maximum number of species possible. In the cases of plant height and winter hardiness, for which one might expect non-linear relationships with naturalisation success (e.g. species of moderate height may be more likely to naturalise than shorter and taller species), we also tested models incorporating quadratic terms. All terms whose inclusion in their respective models resulted in a ΔAIC of -4 or below compared to the intercept-only model were then included into a single saturated model (see Table S1). We selected the conservative ΔAIC cutoff of -4 to ensure that our saturated model was not over-fitted and included only variables that are potentially important for naturalisation success. All models tested included uninformative priors (for residual structure: $V = 1$; for variance structure: $V = 1$, $\nu = 0.002$), and were run for 110,000 iterations, with a burn-in of 10,000 and thinning to every 10th iteration in 10, totalling 10,000 iterations per model.

We then performed model reduction to reach a minimum adequate model. Because of the large number of terms in the saturated model, it was not possible to do this by comparing ΔAIC values for all possible submodels. Therefore, we instead removed terms one at a time from the saturated model, beginning with interaction terms with the highest p -values. We retained only the terms

whose removal from the model yielded an increase in model AIC of >4 . This was repeated for all terms, in the order of decreasing p -value, until a minimal adequate model was reached (Table S2). The model reduction was done using the maximum number of species with complete data for all terms included, that is, 1,879 species. After reaching the reduced minimal adequate model, additional species with data for all remaining terms were added (returning us to 2,073 species).

To assess the quality and predictive value of our minimal adequate model, we performed a 10-fold cross-validation after dividing the data into ten equal subsamples (folds). The model was tested on one test fold after training on the other nine folds using the *predict.MCMCglmm* function in *MCMCglmm*, and this was repeated for each fold. For each test fold, we calculated the True Skill Statistic (TSS; Allouche, Tsoar, & Kadmon, 2006), adjusting the threshold where predicted values were relegated to either 1 (naturalised) or 0 (non-naturalised) to maximise TSS. These calculations were conducted using the *KappaRepet* function in the *BIOMOD* package version 1.1-7.04 (Thuiller, Lafourcade, Engler, & Araújo, 2009). We subsequently measured the mean TSS and standard error across all folds. We also assessed convergence of the model through comparisons to three additional iterations of the model using Gelman and Rubin's convergence diagnostic via the *gelman.diag* function in the *coda* package (Plummer, Best, Cowles, & Vines, 2006).

2.4 Projecting naturalisation success

We used the minimal adequate model to project the probability of naturalisation success in Europe for the 1,583 not-yet-naturalised alien species under recent and future climates (Figure 1c). We used *predict.MCMCglmm*, which allows inclusion of phylogenetic information, to estimate probabilities of naturalisation success for each species. We applied the model to our data once with the recent climatic suitability data and once with the projected future climatic suitability data. Although other model variables, such as nursery availability, may also change in the future, there are no future projections

available for these variables, and we therefore used their current values for future projections.

3 RESULTS

3.1 Changing climatic suitability

Recent median climatic suitability across Europe was 1.32 times larger for naturalised species than for non-naturalised species, averaging 0.029 ($SE = 0.001$) and 0.022 ($SE < 0.001$) respectively (Figure 2a). On average, median climatic suitability in 2050 increased slightly, compared to that under recent climates, to 0.031 ($SE = 0.001$) for naturalised and 0.025 ($SE < 0.001$) for non-naturalised species (Figure 2a,b). The highest recent median climatic suitability of a naturalised species was 0.195 (*Nicotiana glauca*), and that of a non-naturalised species was 0.067 (*Tradescantia spathacea*). These two species also had the highest climatic suitability values in 2050, and both increased; *N. glauca* to 0.248, and *T. spathacea* to 0.160.

3.2 Predictors of naturalisation success

The minimal adequate model of current naturalisation success in Europe retained in the order of importance: naturalised range size outside of Europe, availability in nurseries, recent climatic suitability, sexual system, the interaction between availability in nurseries and sexual system and plant height (Figure 3). Climatic suitability, availability in nurseries and naturalised range size outside of Europe were strongly positively related to naturalisation success in Europe (Figure 4a–c). Dioecious species had on average a slightly higher probability to naturalise than non-dioecious species, particularly at moderate levels of availability in nurseries (Figure 4b). Although naturalisation success increased with plant height in a single-variable model (Table S1), this relationship was weak to absent in the minimal adequate model (Figure 4d). Variance explained due to phylogenetic structure was low, with a posterior mean of 0.015 (Table S3).

The minimal adequate model's predictive value based on 10-fold cross-validation was moderate (Landis & Koch, 1977), with

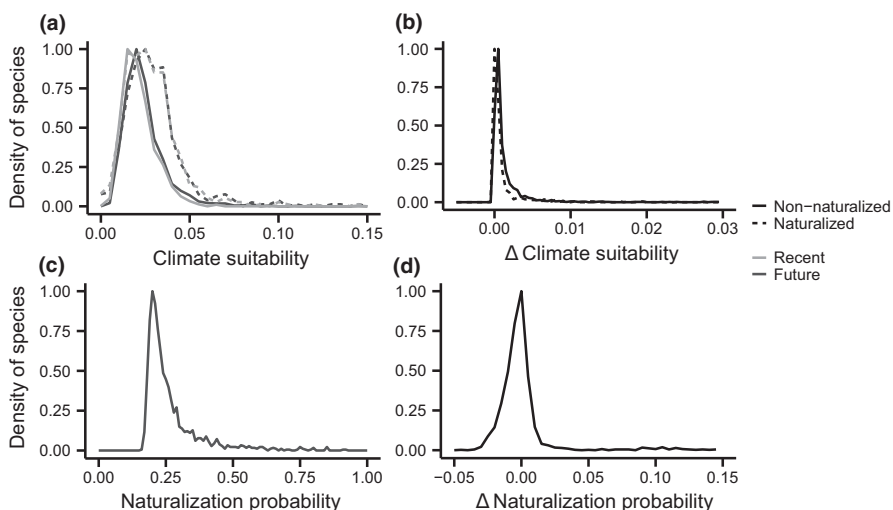


FIGURE 2 Density curves showing (a) recent and future (2050) climatic suitability (grey and black, respectively), for species already naturalised in Europe (dashed lines) and not-yet-naturalised species (solid lines); (b) individual species changes in climatic suitability between recent and future climates for naturalised and non-naturalised species; (c) future naturalisation probability (for non-naturalised species only) and (d) individual species changes in naturalisation probability between recent and future climates

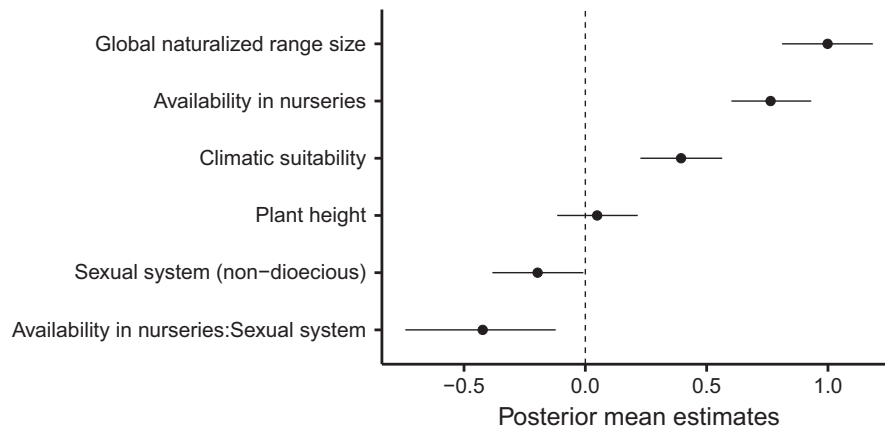


FIGURE 3 Posterior mean estimates plus 95% credible intervals for terms included in the minimal adequate model. For exact values, refer to Table S3. Positive estimates indicate positive effects, and negative values indicate negative effects. Climatic suitability refers to species median climatic suitability in Europe. Global naturalised range size is the number of regions, where naturalised outside of Europe. Availability in nurseries is the number of nurseries in Europe where a species is available for sale. Plant height is the maximum height reported. Sexual system refers to whether a species is non-dioecious or dioecious

TSS = 0.45 ($SE = 0.03$). Gelman and Rubin's convergence diagnostic for our model and additional iterations was 1.00, indicating convergence (Brooks & Gelman, 1998).

3.3 Changing naturalisation probability for non-naturalised species

Changes in naturalisation probability between recent climates and projected 2050 climates ranged from a decrease of 0.137 to an increase of 0.421 (with the highest increase for *Nopalea cochenillifera*; Table S4). Forty-one species experienced increases in naturalisation probability greater than 0.1, whereas only one species saw a decrease in naturalisation probability greater than 0.1 (*Penstemon gracilis*). *Tamarus indica* had the highest future naturalisation probability at 0.917, and 20 other species had naturalisation probabilities >0.7 (Table S4). Projected future naturalisation probability in Europe averaged across all non-naturalised ornamental species was 0.266 ($SE = 0.003$; Figure 2c), increasing slightly from 0.244 ($SE = 0.003$) under recent climates (Figure 2d). A complete list of species' naturalisation probabilities is given in Table S5.

4 DISCUSSION

We found that naturalisation success of ornamental alien plants in Europe is positively related to climatic suitability, availability in nurseries and naturalisation success elsewhere. While we did not find a substantial increase in the average naturalisation potential under future compared to recent climates across all species, there were nevertheless many species with substantial increases in naturalisation probability. Importantly, our analysis identified species for which an invasion debt may exist now, given their naturalisation probability under recent climates, as well as in the future.

4.1 Predictors of naturalisation success

The three main predictors of naturalisation success we identified are climatic suitability, availability in nurseries (i.e. propagule pressure) and naturalisation success elsewhere. While the importance of climatic suitability is widely acknowledged, few studies have tested it explicitly. The ones that did test it also demonstrated its importance (Feng et al., 2016; Mayer et al., 2017). The significance of propagule pressure for plant invasions is well-established (Bucharová & van Kleunen, 2009; Dehnen-Schmutz, Touza, Perrings, & Williamson, 2007b; Feng et al., 2016; Hanspach et al., 2008; Lockwood et al., 2005; Pyšek et al., 2009b), and the same is true for the effect of naturalisation or invasion success elsewhere (Klonner, Fischer, Essl, & Dullinger, 2016; Kolar & Lodge, 2001; Mayer et al., 2017; Reichard & Hamilton, 1997). Compared to those other studies, which included naturalisation elsewhere primarily as a binary metric (yes, no), our study shows that more detailed information on the number of regions where a species is naturalised further improves the predictive value of naturalisation elsewhere (i.e. Figure 4c).

Height and sexual system are the only species traits that were retained in the minimal adequate model. Height had a positive effect in the single-variable model. However, although it improved the overall fit of the multiple-variable model, its effect was no longer significant. Results of previous studies are mixed, but when height had a significant effect, it usually was a positive one (Bucharová & van Kleunen, 2009; Hanspach et al., 2008; Maurel et al., 2016). This suggests that at least for some groups of plants, height improves competitive ability and seed-dispersal (Thompson, Letten, Tamme, Edwards, & Moles, 2017). Dioecious species were slightly more likely to naturalise than non-dioecious species (Figure 4b). This is surprising as previous studies did not find such an effect (e.g. Dawson, Burslem, & Hulme, 2009; Milbau & Stout, 2008; Pyšek et al., 2009a, 2015), and because dioecious species—having separate male and

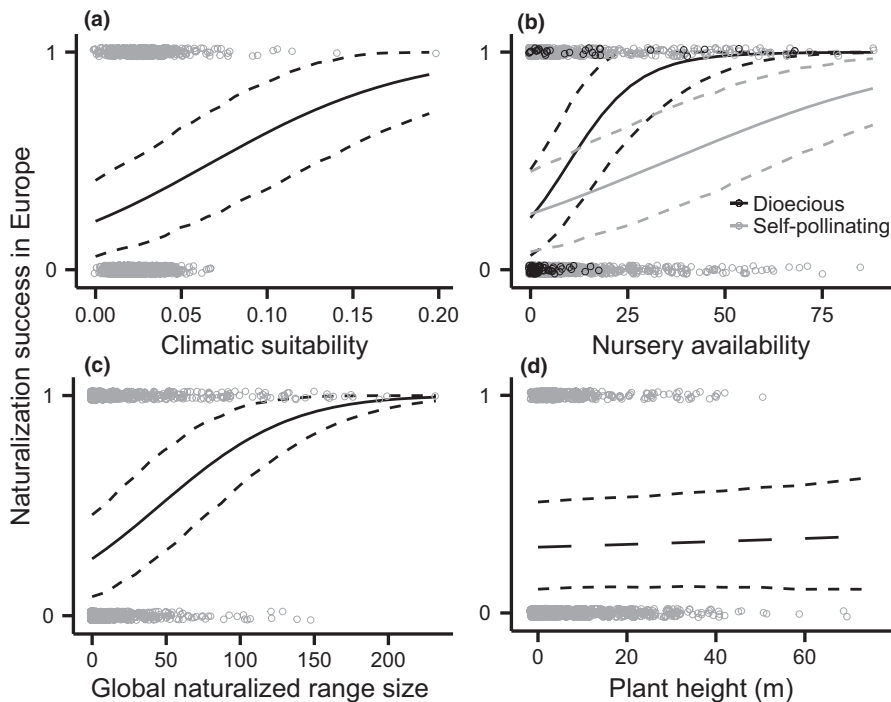


FIGURE 4 Relationships of naturalisation success in Europe and variables included in the minimal adequate model. Data points were jittered to increase visibility. Lines represent model predictions, across the given variable range with all other model terms set to zero (after scaling or centring). Dashed lines represent 95% confidence intervals. Climatic suitability (a), the median value for Europe, is presented on a 0–1 scale. Availability in nurseries (b), represents the number of nurseries across Europe where a species is sold, for both dioecious (black) and non-dioecious (grey) species. Global naturalised range size (c) is the number of regions outside of Europe, where a species is already naturalised. Plant height (d) is the maximum species height, and the non-significance of plant height effect is denoted with a long-dashed line

female individuals—cannot self-fertilise and thus need to be introduced in large numbers to naturalise. Consistent with this, the positive effect of dioecy on naturalisation was not apparent for species with low availabilities in nurseries (Figure 4b). Possibly, the positive effect of dioecy on naturalisation success at higher availabilities in nurseries was actually due to effects of other traits, such as wind-pollination, that are associated with dioecy (Renner, 2014).

While native range size and absence of storage organs were significant in single-variable analyses (Table S1), their significances disappeared in the multiple-variable analysis. Growth form, vegetative propagation, propagation by seeds and hardiness were not significant in any model. Some of these species characteristics, however, have been found to affect naturalisation or invasion success in studies focussing on smaller regions (Haeuser, Dawson, & van Kleunen, 2017; Hanspach et al., 2008; Kolar & Lodge, 2001; Maurel et al., 2016). The absence of significance in our study might reflect potential correlations with factors retained in the model. Furthermore, it may reflect context-specificity and invasion-stage dependence of some species characteristics (Pyšek & Richardson, 2007; Pyšek et al., 2009a; Williamson, 2006).

4.2 Model limitations

Our analyses of European naturalisation success include many variables previously reported to be associated with naturalisation success. Nevertheless, the projections of naturalisation potential of the final model could still be improved. Although we included over 2,000 ornamental species and many potential predictors, many other species and predictors could not be included due to insufficient data. For example, we did not have data on time since introduction, which is usually

associated with naturalisation success (e.g. Bucharová & van Kleunen, 2009; Feng et al., 2016; Harris, Murray, Hose, & Hamilton, 2007).

Our model projections of future naturalisation were only based on projections for future climatic suitability. It is likely that other variables kept static, such as availability in nurseries and extent of naturalisation elsewhere may also be subject to change in the future. Furthermore, as land use is important for the success of alien species (Chytrý et al., 2009, 2012), future models should aim to also include information on current land use and land-use-change scenarios. Despite the limitations of the current model, we believe our approach offers a robust basis for identifying species at high risk for naturalisation under future climates.

4.3 Future naturalisation risk of non-naturalised ornamental species

Our projections identified several species with very high future probabilities of naturalisation. Species with probabilities >0.8 include *Artocarpus altilis*, *Albizia lebeck*, *Caesalpinia pulcherrima*, *Cosmos sulphureus*, *Emilia sonchifolia*, *Gomphrena globosa*, *Tamarindus indica* and *Tradescantia spathacea*. With the exception of *T. spathacea*, all of these species are already naturalised in over 100 regions outside of Europe (van Kleunen et al., 2015). Possibly, these species have not yet naturalised in Europe because they were introduced only recently or into parts of Europe where climates or habitat are not yet suitable, or they face resistance by biological barriers, such as competition (e.g. Carboni et al., 2017). With climate change, however, these species will likely pose the greatest risk for naturalisation in Europe in the future.

The aim of our study was to identify ornamental species with naturalisation risk at the broad European level and should be targeted for e.g. European Union-level regulations. Our approach

does not allow us to identify naturalisation risks in different parts of Europe and also cannot distinguish species that will merely naturalise and those that will become invasive and have negative impacts. Therefore, those species with indications of high naturalisation probability ought to be investigated further in terms of local climatic suitability and propagule pressure to identify regions in Europe where they pose high risks (see e.g. Mayer et al., 2017).

Climatic suitability and naturalisation probabilities of not-yet naturalised ornamentals in Europe are projected to increase on average only slightly by 2050. Nevertheless, some species will show large increases in naturalisation risk (Table S4). Among the species we identify as having a high naturalisation probability under recent and/or future climates, some already have been reported in Europe as garden escapees without forming persistent populations (i.e. are casuals; *Acer palmatum*, *Dodonaea viscosa*, *Gomphrena globosa*, *Perovskia atriplicifolia* and *Physostegia virginiana*; www.europe-aliens.org). Curbing the cultivation of these ornamental species in Europe should be prioritised to prevent further naturalisations and possible invasions.

5 CONCLUSIONS

The horticultural industry is still growing (Bradley et al., 2012; van Kleunen et al., 2018), and new species continue to be introduced or more intensively traded regardless of their invasion potential (Drew, Anderson, & Andow, 2010). Recently, it was shown that Europe has a relatively high invasion threat but also has the capacity to proactively or reactively respond (Early et al., 2016; Turbelin, Malamud, & Francis, 2017). Proactive responses could be further improved by forecasting future threats (Hulme et al., 2017), as we did here. Knowler and Barbier (2005) showed that taxing of imports and sales of invasive species would significantly reduce further invasions. Extending this option beyond already-invasive species to those deemed high-risk potential invaders, such as those identified in this study, would likely reduce their use and subsequently their naturalisation potential. None of the species we list here are currently present on the list of invasive alien species of European Union concern (European Union, 2014). The methods we use here offer a useful approach for informing proactive European invasive alien species policies.

ACKNOWLEDGEMENTS

We thank Hanno Seebens for providing GRIN native range-size data, Ingolf Kühn and Jan Hanspach for providing EGF species-characteristic data, and Ingolf Kühn for comments on a previous manuscript version. We thank Jos Barlow, Rafael Zenni and two anonymous reviewers for many helpful suggestions. This research was funded by the ERA-Net BiodivERsA, with the national funders ANR (French National Research Agency), DFG (German Research Foundation; to M.v.K. and W.D.) and FWF (Austrian Science Fund), part of the 2012–2013 BiodivERsA call for research proposals. P.P. and J.P. acknowledge grants of Centre of Excellence PLADIAS, no. 14-15414S (Czech Science Foundation), long-term research development project RVO 67985939 (Czech Academy of Sciences) and NAKI II project (DG16P02M041).

AUTHORS' CONTRIBUTIONS

E.H., M.v.K. and W.D. designed the study, with input from W.T., S.D., S.B., O.B., M.C., L.C., I.D., F.E., G.K., D.M., T.M., M.P. and M.V.T. M.v.K., W.D., F.E., H.K., J.P., P.P., P.W. and M.W. compiled the GLONAF database. C.R. compiled the phylogeny. I.K. compiled the EGF species characteristic data. SVV and MH compiled the nursery availability data. EH conducted the analyses and wrote the manuscript. All authors contributed to the manuscript and approved the final version for publication.

ORCID

Emily Haeuser  <http://orcid.org/0000-0003-2179-2601>
 Wayne Dawson  <http://orcid.org/0000-0003-3402-0774>
 Svenja Block  <http://orcid.org/0000-0002-8215-3849>
 Wilfried Thuiller  <http://orcid.org/0000-0002-5388-5274>
 Stefan Dullinger  <http://orcid.org/0000-0003-3919-0887>
 Oliver Bossdorf  <http://orcid.org/0000-0001-7504-6511>
 Marta Carboni  <http://orcid.org/0000-0002-9348-4758>
 Luisa Conti  <http://orcid.org/0000-0001-8047-1467>
 Günther Klöner  <http://orcid.org/0000-0002-5237-2231>
 Franz Essl  <http://orcid.org/0000-0001-8253-2112>
 Dietmar Moser  <http://orcid.org/0000-0002-2745-7508>
 Matthew V. Talluto  <http://orcid.org/0000-0001-5188-7332>
 Holger Kreft  <http://orcid.org/0000-0003-4471-8236>
 Jan Pergl  <http://orcid.org/0000-0002-0045-1974>
 Petr Pyšek  <http://orcid.org/0000-0001-8500-442X>
 Martin Hermy  <http://orcid.org/0000-0002-5403-0139>
 Patrick Weigelt  <http://orcid.org/0000-0002-2485-3708>
 Marten Winter  <http://orcid.org/0000-0002-9593-7300>
 Cristina Roquet  <http://orcid.org/0000-0001-8748-3743>
 Mark van Kleunen  <http://orcid.org/0000-0002-2861-3701>

REFERENCES

- Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, 43, 1223–1232. <https://doi.org/10.1111/j.1365-2664.2006.01214.x>
- Bradley, B. A., Blumenthal, D. M., Early, R., Grosholz, E. D., Lawler, J. J., Miller, L. P., ... Olden, J. D. (2012). Global change, global trade, and the next wave of plant invasions. *Frontiers in Ecology and the Environment*, 10, 20–28. <https://doi.org/10.1890/110145>
- Brooks, S. P., & Gelman, A. (1998). General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, 7, 434–455.

- Brummit, R. (2001). *World geographical scheme for recording plant distributions* (2nd ed.). Pittsburgh, PA: Hunt Institute for Botanical Documentation.
- Bucharová, A., & van Kleunen, M. (2009). Introduction history and species characteristics partly explain naturalization success of North American woody species in Europe. *Journal of Ecology*, *97*, 230–238. <https://doi.org/10.1111/j.1365-2745.2008.01469.x>
- Carboni, M., Guégue, M., Barros, C., Georges, D., Boulangeat, I., Douzet, R., ... Bossdorf, O. (2017). Simulating plant invasion dynamics in mountain ecosystems under global change scenarios. *Global Change Biology*, <https://doi.org/10.1111/gcb.13879>
- Cayuela, L., & Oksanen, J. (2016). Taxonstand: Taxonomic Standardization of Plant Species Names. R package version 2.1. Retrieved from <https://CRAN.R-project.org/package=Taxonstand>
- Chytrý, M., Pyšek, P., Wild, J., Pino, J., Maskell, L. C., & Vilà, M. (2009). European map of alien plant invasions based on the quantitative assessment across habitats. *Diversity and Distributions*, *15*, 98–107. <https://doi.org/10.1111/j.1472-4642.2008.00515.x>
- Chytrý, M., Wild, J., Pyšek, P., Jarošík, V., Dendoncker, N., Reginster, I., ... Settele, J. (2012). Projecting trends in plant invasions in Europe under different scenarios of future land-use change. *Global Ecology and Biogeography*, *21*, 75–87. <https://doi.org/10.1111/j.1466-8238.2010.00573.x>
- Cullen, J., Knees, S. G., Cubey, H. S., & Shaw, J. M. H. (Eds.) (2012). *The European Garden Flora Flowering Plants: A Manual for the Identification of Plants Cultivated in Europe. Both Out-of-Doors and Under Glass*. Chicago, IL: The University of Chicago Press.
- Dawson, W., Burslem, D. F. R. P., & Hulme, P. E. (2009). Factors explaining alien plant invasion success in a tropical ecosystem differ at each stage of invasion. *Journal of Ecology*, *97*, 657–665. <https://doi.org/10.1111/j.1365-2745.2009.01519.x>
- Dehnen-Schmutz, K., Touza, J., Perrings, C., & Williamson, M. (2007a). A century of the ornamental plant trade and its impact on invasion success. *Diversity and Distributions*, *13*, 527–534. <https://doi.org/10.1111/j.1472-4642.2007.00359.x>
- Dehnen-Schmutz, K., Touza, J., Perrings, C., & Williamson, M. (2007b). The horticultural trade and ornamental plant invasions in Britain. *Conservation Biology*, *21*, 224–231. <https://doi.org/10.1111/j.1523-1739.2006.00538.x>
- Drew, J., Anderson, N., & Andow, D. (2010). Conundrums of a complex vector for invasive species control: A detailed examination of the horticultural industry. *Biological Invasions*, *12*, 2837–2851. <https://doi.org/10.1007/s10530-010-9689-8>
- Dullinger, I., Wessely, J., Bossdorf, O., Dawson, W., Essl, F., Gattringer, A., ... Pergl, J. (2017). Climate change will increase the naturalization risk from garden plants in Europe. *Global Ecology and Biogeography*, *26*, 3–53.
- Early, R., Bradley, B. A., Dukes, J. S., Lawler, J. J., Olden, J. D., Blumenthal, D. M., ... Sorte, C. J. (2016). Global threats from invasive alien species in the twenty-first century and national response capacities. *Nature Communications*, *7*, 12485. <https://doi.org/10.1038/ncomms12485>
- Essl, F., Dullinger, S., Rabitsch, W., Hulme, P. E., Hülber, K., Jarošík, V., ... Vilà, M. (2011). Socioeconomic legacy yields an invasion debt. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 203–207. <https://doi.org/10.1073/pnas.1011728108>
- European Union. (2014). *Regulation (EU) No 1143/2014 of the European Parliament and of the Council of 22 October 2014 on the prevention and management of the introduction and spread of invasive alien species*. OJ L 317 (4.11.2014), 35–55.
- Feng, Y., Maurel, N., Wang, Z., Ning, L., Yu, F. H., van Kleunen, M., & Fleishman, E. (2016). Introduction history, climatic suitability, native range size, species traits and their interactions explain establishment of Chinese woody species in Europe. *Global Ecology and Biogeography*, *25*, 1356–1366. <https://doi.org/10.1111/geb.12497>
- Gallien, L., Thuiller, W., Fort, N., Boleda, M., Alberto, F. J., Rioux, D., ... Lavergne, S. (2016). Is there any evidence for rapid, genetically-based, climatic-niche expansion in the invasive common ragweed? *PLoS ONE*, *11*, e0152867. <https://doi.org/10.1371/journal.pone.0152867>
- GBIF. (2018). GBIF Home Page. Available from: <https://www.gbif.org>
- Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm {R} Package. *Journal of Statistical Software*, *33*, 1–22.
- Haeuser, E., Dawson, W., Thuiller, W., Dullinger, S., Block, S., Bossdorf, O., ... van Kleunen, M. (2018). Data from: European ornamental garden flora as an invasion debt under climate change. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.2s25t0g>
- Haeuser, E., Dawson, W., & van Kleunen, M. (2017). The effects of climate warming and disturbance on the colonization potential of ornamental alien plant species. *Journal of Ecology*, *105*, 1698–1708. <https://doi.org/10.1111/1365-2745.12798>
- Hanspach, J., Kühn, I., Pyšek, P., Boos, E., & Klotz, S. (2008). Correlates of naturalization and occupancy of introduced ornamentals in Germany. *Perspectives in Plant Ecology, Evolution and Systematics*, *10*, 241–250. <https://doi.org/10.1016/j.ppees.2008.05.001>
- Harris, C. J., Murray, B. R., Hose, G. C., & Hamilton, M. A. (2007). Introduction history and invasion success in exotic vines introduced to Australia. *Diversity and Distributions*, *13*, 467–475. <https://doi.org/10.1111/j.1472-4642.2007.00375.x>
- Hayes, K. R., & Barry, S. C. (2008). Are there any consistent predictors of invasion success? *Biological Invasions*, *10*, 483–506. <https://doi.org/10.1007/s10530-007-9146-5>
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*, 1965–1978. [https://doi.org/10.1002/\(ISSN\)1097-0088](https://doi.org/10.1002/(ISSN)1097-0088)
- Hulme, P. E., Brundu, G., Carboni, M., Dehnen-Schmutz, K., Dullinger, S., Early, R., ... Kühn, I. (2017). Integrating invasive species policies across ornamental horticulture supply-chains to prevent plant invasions. *Journal of Applied Ecology*, *55*, 92–98. <https://doi.org/10.1111/1365-2664.12953>
- Karger, D. N., Conrad, O., Böhrner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., ... Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*, 170122. <https://doi.org/10.1038/sdata.2017.122>
- Klonner, G., Dullinger, I., Wessely, J., Bossdorf, O., Carboni, M., Dawson, W., ... Kreft, H. (2017). Will climate change increase hybridization risk between potential plant invaders and their congeners in Europe? *Diversity and Distributions*, *23*, 934–943. <https://doi.org/10.1111/ddi.12578>
- Klonner, G., Fischer, S., Essl, F., & Dullinger, S. (2016). A source area approach demonstrates moderate predictive ability but pronounced variability of invasive species traits. *PLoS ONE*, *11*, 1–14.
- Knowler, D., & Barbier, E. (2005). Importing exotic plants and the risk of invasion: Are market-based instruments adequate? *Ecological Economics*, *52*, 341–354. <https://doi.org/10.1016/j.ecolecon.2004.06.019>
- Kolar, C. S., & Lodge, D. M. (2001). Progress in invasion biology. *Trends in Ecology & Evolution*, *16*, 199–204. [https://doi.org/10.1016/S0169-5347\(01\)02101-2](https://doi.org/10.1016/S0169-5347(01)02101-2)
- Kowarik, I., Pyšek, P., Prach, K., Rejmánek, M., & Wade, M. (1995). *Time lags in biological invasions with regard to the success and failure of alien species. Plant invasions: General aspects and special problems*. Workshop held at Kostelec nad Černými lesy, Czech Republic, 16–19 September 1993, pp. 15–38.
- Küster, E. C., Kühn, I., Bruehlheide, H., & Klotz, S. (2008). Trait interactions help explain plant invasion success in the German flora. *Journal of Ecology*, *96*, 860–868. <https://doi.org/10.1111/j.1365-2745.2008.01406.x>
- Landis, J. R., & Koch, G. G. (1977). The measurement of observer agreement for categorical data. *Biometrics*, *33*, 159–174. <https://doi.org/10.2307/2529310>

- Lockwood, J. L., Cassey, P., & Blackburn, T. (2005). The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution*, 20, 223–228. <https://doi.org/10.1016/j.tree.2005.02.004>
- Maurel, N., Hanspach, J., Kühn, I., Pyšek, P., & van Kleunen, M. (2016). Introduction bias affects relationships between the characteristics of ornamental alien plants and their naturalization success. *Global Ecology and Biogeography*, 25, 1500–1509. <https://doi.org/10.1111/geb.12520>
- Mayer, K., Haeuser, E., Dawson, W., Essl, F., Kreft, H., Pergl, J., ... van Kleunen, M. (2017). Current and future local naturalization potential of ornamental species planted in public green spaces and private gardens. *Biological Invasions*, 12, 3613–3627. <https://doi.org/10.1007/s10530-017-1594-y>
- Millbau, A., & Stout, J. C. (2008). Factors associated with alien plants transitioning from casual, to naturalized, to invasive. *Conservation Biology*, 2, 308–317. <https://doi.org/10.1111/j.1523-1739.2007.00877.x>
- Pergl, J., Sádlo, J., Petřík, P., Danihelka, J., Chrtek, J. Jr, Hejda, M., ... Pyšek, P. (2016). Dark side of the fence: Ornamental plants as a source for spontaneous flora of the Czech Republic. *Preslia*, 88, 163–184.
- Pheloung, P. C., Williams, P. A., & Halloy, S. R. (1999). A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. *Journal of Environmental Management*, 57, 239–251. <https://doi.org/10.1006/jema.1999.0297>
- Plummer, M., Best, N., Cowles, K., & Vines, K. (2006). CODA: Convergence diagnosis and output analysis for MCMC. *R News*, 6, 7–11.
- Pyšek, P., Jarošík, V., Pergl, J., Randall, R., Chytrý, M., Kühn, I., ... Sádlo, J. (2009a). The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. *Diversity and Distributions*, 15, 891–903.
- Pyšek, P., Krivanek, M., & Jarošík, V. (2009b). Planting intensity, residence time, and species traits determine invasion success of alien woody species. *Ecology*, 90, 2734–2744.
- Pyšek, P., Manceur, A. M., Alba, C., McGregor, K. F., Pergl, J., Štajerová, K., ... Lučanová, M. (2015). Naturalization of central European plants in North America: Species traits, habitats, propagule pressure, residence time. *Ecology*, 96, 762–774.
- Pyšek, P., Pergl, J., Essl, F., Lenzner, B., Dawson, W., Kreft, H., ... van Kleunen, M. (2017). Naturalized alien flora of the world: Species diversity, taxonomic and phylogenetic patterns, geographic distribution and global hotspots of plant invasion. *Preslia*, 89, 203–274.
- Pyšek, P., & Richardson, D. M. (2007). Traits associated with invasiveness in alien plants: Where do we stand? In W. Nentwig (Ed.), *Biological invasions, ecological studies*, Vol. 193 (pp. 97–125). Berlin & Heidelberg: Springer-Verlag.
- R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Core Team.
- Razanajatovo, M., Maurel, N., Dawson, W., Essl, F., Kreft, H., Pergl, J., ... Van Kleunen, M. (2016). Plants capable of selfing are more likely to become naturalized. *Nature Communications*, 7, 13313. <https://doi.org/10.1038/ncomms13313>
- Reichard, S. H., & Hamilton, C. W. (1997). Predicting invasions of woody plants introduced to North America. *Conservation Biology*, 11, 193–203. <https://doi.org/10.1046/j.1523-1739.1997.95473.x>
- Renner, S. S. (2014). The relative and absolute frequencies of angiosperm sexual systems: Dioecy, monoecy, gynodioecy, and an updated online database. *American Journal of Botany*, 101, 1–9.
- Richardson, D. M., & Pyšek, P. (2012). Naturalization of introduced plants: Ecological drivers of biogeographic patterns. *New Phytologist*, 196, 383–396. <https://doi.org/10.1111/j.1469-8137.2012.04292.x>
- Richardson, D. M., Pyšek, P., Rejmánek, M., Barbour, M. G., Panetta, F. D., & West, C. J. (2000). Naturalization and invasion of alien plants: Concepts and definitions. *Diversity and Distributions*, 6, 93–107. <https://doi.org/10.1046/j.1472-4642.2000.00083.x>
- Roquet, C., Thuiller, W., & Lavergne, S. (2012). Europe PMC Funders Group Building megaphylogenies for macroecology : Taking up the challenge. *Ecography*, 36, 13–26.
- Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1, 103–113. <https://doi.org/10.1111/j.2041-210X.2010.00012.x>
- Secretariat of the Convention on Biological Diversity (CBD). (2000). *Alien species that threaten ecosystems, habitats or species*. UNEP/CBD/COP/5/8, Secretariat of the Convention on Biological Diversity, Nairobi, Kenya.
- Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., ... Bacher, S. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, 8, 14435. <https://doi.org/10.1038/ncomms14435>
- Thompson, F. J., Letten, A. D., Tamme, R., Edwards, W., & Moles, A. T. (2017). Can dispersal investment explain why tall plant species achieve longer dispersal distances than short plant species? *New Phytologist*, 217, 407–415. <https://doi.org/10.1111/nph.14735>
- Thuiller, W., Georges, D., & Engler, R. (2016). biomod2: Ensemble platform for species distribution modeling. Retrieved from <https://CRAN.R-project.org/package=biomod2>
- Thuiller, W., Lafourcade, B., Engler, R., & Araújo, M. B. (2009). BIOMOD – A platform for ensemble forecasting of species distributions. *Ecography*, 32, 369–373. <https://doi.org/10.1111/j.1600-0587.2008.05742.x>
- Turbelin, A. J., Malamud, B. D., & Francis, R. A. (2017). Mapping the global state of invasive alien species: Patterns of invasion and policy responses. *Global Ecology and Biogeography*, 26, 78–92. <https://doi.org/10.1111/geb.12517>
- Van der Veken, S., Hermy, M., Vellend, M., Knäpen, A., & Verheyen, K. (2008). Garden plants get a head start on climate change. *Frontiers in Ecology and the Environment*, 6, 212–216. <https://doi.org/10.1890/070063>
- van Kleunen, M., Dawson, W., Essl, F., Pergl, J., Winter, M., Weber, E., ... Antonova, L. A. (2015). Global exchange and accumulation of non-native plants. *Nature*, 525, 100–103. <https://doi.org/10.1038/nature14910>
- van Kleunen, M., Dawson, W., Schlaepfer, D. R., Jeschke, J. M., & Fischer, M. (2010). Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. *Ecology Letters*, 13, 947–958.
- van Kleunen, M., Essl, F., Pergl, J., Brundu, G., Carboni, M., Dullinger, S., ... Kueffer, C. (2018). The changing role of ornamental horticulture in alien plant invasions. *Biological Reviews*. <https://doi.org/10.1111/brv.12402>
- Walther, G. R., Roques, A., Hulme, P. E., Sykes, M. T., Pyšek, P., Kühn, I., ... Czucz, B. (2009). Alien species in a warmer world: Risks and opportunities. *Trends in Ecology & Evolution*, 24, 686–693. <https://doi.org/10.1016/j.tree.2009.06.008>
- WCSP. (2017). *World checklist of selected plant families*. Kew: Facilitated by the Royal Botanic Gardens.
- Wiersema, J. H. (1995). Taxonomic information on cultivated plants in the USDA/ARS Germplasm Resources Information Network (GRIN). *Acta Horticulturae*, 413, 109–116. <https://doi.org/10.17660/ActaHortic.1995.413.16>
- Williamson, M. (2006). Explaining and predicting the success of invading species at different stages of invasion. *Biological Invasions*, 8, 1561–1568. <https://doi.org/10.1007/s10530-005-5849-7>