

Introduction history, climatic suitability, native range size, species traits and their interactions explain establishment of Chinese woody species in Europe

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ABSTRACT

Aim A major challenge in ecology is to understand how multiple causal factors, which may interact, drive success of non native plants in new ranges. In this study we addressed the role of introduction history, climatic suitability, native range size, species traits and their interactions in the establishment of Chinese woody species in Europe.

Location China (native range), Europe (new range).

Methods We tested whether establishment of 449 Chinese woody species in Europe was associated with residence time (time since earliest planting), planting frequency, climatic suitability, native range size and species traits. We also considered possible nonlinear effects and interactions among these variables. For the 38 species that have established in Europe, we further tested whether these variables and interactions explained their establishment in multiple European countries.

Results Establishment of the 449 species in Europe was positively associated with residence time, planting frequency and climatic suitability. Except residence time, these factors were also positively associated with establishment of the 38 species in multiple countries. None of the traits tested had statistically significant main effects on establishment in Europe, but, for the established species, longer flowering period and having compound leaves were positively associated with establishment in multiple countries. The positive association between establishment in Europe and residence time was stronger for evergreen than for deciduous species. In addition, evergreens, unlike deciduous species, showed a positive association between establishment in Europe and fruiting duration. Moreover, establishment in multiple countries was positively associated with planting frequency for species with compound leaves but not for species with simple leaves, and the association between the establishment and fruiting duration changed from negative to moderately positive as climatic suitability increased.

Main conclusions Introduction history and climatic suitability explain most of the variation in establishment, and modulate the role of species traits, such as leaf retention, leaf type and fruiting duration.

Keywords

Biomod2, climatic niches, dispersal, gardens, maximum height, ornamental plants, plant invasion, propagule pressure, spread.

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INTRODUCTION

More than 13,000 plant species have established self-sustaining populations outside their native range (van Kleunen *et al.*, 2015a). Some of them have become invasive and pose a threat to natural ecosystems. Given that only few of the introduced non-native plant species have established and fewer have become invasive in new ranges, a major question in ecology is why some non-native plants succeed and others fail (Kolar & Lodge, 2001)? Addressing this question has been challenging, because there are multiple potential causal factors (e.g. introduction history, environmental factors and species traits) which may interact (Theoharides & Dukes, 2007; Pyšek *et al.*, 2015), and invasions have multiple stages (Kolar & Lodge, 2001, 2002; Blackburn *et al.*, 2011). Therefore, it is essential to understand how multiple factors interact to explain the success of non-native plants at different invasion stages (Richardson & Pyšek, 2012; Kempel *et al.*, 2013; van Kleunen *et al.*, 2015b).

The introduction history of a non-native plant species, i.e. when the species was introduced and how frequently it has been planted, affects its probability of establishing populations in the wild (Bucharova & van Kleunen, 2009; Pyšek *et al.*, 2009). Due to a dearth of data on the year of introduction, however, studies have not used the year of introduction but the year of first record in the wild. This measure has the disadvantage that it excludes those species that failed to establish after introduction (Kowarik, 1995). Similarly, very few studies (e.g. Bucharova & van Kleunen, 2009) have used measures reflecting actual plantings to assess the role of planting frequency.

Many environmental variables also affect the success of non-native plants (Theoharides & Dukes, 2007). Climate is a major determinant of whether non-native plants can survive, grow and reproduce, and thus establish and spread in new regions (Richardson & Pyšek, 2012). Niche-based species distribution models (SDMs), parameterized with climatic data from the native range, have been frequently used to assess occurrence probability of non-native plants in new ranges (Thuiller *et al.*, 2005). However, to the best of our knowledge, the role of climatic suitability has not been tested explicitly by correlating the occurrence probability predicted from SDMs with actual establishment of non-native plants in new ranges.

Traits reflect plant ecological strategies and determine how plants respond to abiotic and biotic environmental factors (Pérez Harguindeguy *et al.*, 2013). Therefore, traits are likely to play major roles in the invasion process (Baker, 1974; Pyšek & Richardson, 2007; van Kleunen *et al.*, 2010). Examples of potentially important traits are those affecting light and resource capture (e.g. height, leaf traits), reproduction (e.g. flowering phenology) and dispersal (e.g. height; Thomson *et al.*, 2011). Despite intensive research, the role of traits in predicting establishment is still not clear (Daehler, 2003; Pyšek & Richardson, 2007; van Kleunen *et al.*, 2010, 2011; Thompson & Davis, 2011). In addition, native range size, as

a biogeographical characteristic reflecting a species' environmental tolerance, may also explain how widely non-native plants establish (Hui *et al.*, 2011).

Despite evidence for the roles of multiple causal factors in the invasion process, studies have found partly inconsistent results (Pyšek & Richardson, 2007; Richardson & Pyšek, 2012). This is likely because the role of certain factors, in particular that of species traits, depends on the invasion stage (Kolar & Lodge, 2001, 2002) and context (Daehler, 2003; Moles *et al.*, 2008; van Kleunen *et al.*, 2015b). However, few studies have tested this explicitly by exploring whether the multiple factors interact (but see Küster *et al.*, 2008). Furthermore, although most studies implicitly assume that the relation between establishment and causal factors is linear, it may be nonlinear (van Kleunen *et al.*, 2015b).

We tested whether establishment of 449 Chinese woody species in Europe was associated with residence time (time since first planting record), planting frequency, climatic suitability, species traits and native range size. We considered linear and nonlinear associations and interactions among these variables. In addition, for the 38 species that have established in Europe, we tested whether their establishment in multiple European countries, reflecting either multiple independent establishment events and/or spread from one country to the other, was associated with the same variables and interactions.

METHODS

Data compilation

We compiled data on 449 woody species (276 shrubs, 142 trees and 31 lianas, representing 65 families) that have been deliberately introduced from their native range in China (or Japan for a few species; Appendix S1 in Supporting Information) to Europe for ornamental purposes (i.e. planted in gardens) since the 16th century (Goeze, 1916). The DAISIE database (<http://www.europealiens.org/>, last accessed in July 2014) indicated that 38 species, representing 17 families, have established in at least one of the 15 countries in Europe for which we had data on planting frequency (see below). We calculated residence time of each of the 449 species in Europe by subtracting the year of its earliest planting, as reported in Goeze (1916) and Bärtels (2001), from 2014. As a measure of a species' planting frequency in Europe, we calculated the proportion of the gardens (i.e. botanical gardens, arboretums, and castle, public and private parks) listed in Bärtels *et al.* (1982) where the species was planted (see Fig. S3 in Appendix S2 for locations of the gardens). Planting data are available for a total of 198 gardens covering 15 European countries: Austria (16 gardens listed), Belgium (3), Czech Republic (28), Denmark (3), Finland (5), France (4), Germany (103), Hungary (4), the Netherlands (10), Norway (2), Poland (5), Romania (1), Slovakia (2), Sweden (4) and Switzerland (8). Similarly, we assigned a value of planting frequency in each country separately for each of the 38 species that have established in Europe.

Table 1 Fourteen explanatory variables included in our analyses

Variable	Explanation	Source
Introduction history		
Residence time	Years since earliest known planting in Europe	Goeze (1916), Bartels (2001)
Planting frequency	Proportion of gardens in which the species was planted in a region*	Bartels <i>et al.</i> (1982)
Climatic suitability	Maximum climatic suitability in a region (between 0 and 1)*	Bioclimatic niche modelling
Native range size	Proportion of grid cells in China where a species occurs	Fang <i>et al.</i> (2011)
Species traits		
Maximum height	Maximum height (m)	Flora of China, Hortipedia
Earliest flowering month	From 1 (January) to 12 (December)	Flora of China
Flowering duration	Number of flowering months	Flora of China
Earliest fruiting month	From 1 (January) to 12 (December)	Flora of China
Fruiting duration	Number of fruiting months	Flora of China
Growth form	Tree, shrub, liana	Flora of China
Sexual system	Dioecious, hermaphrodite, monoecious	Flora of China
Leaf retention	Deciduous, evergreen	Flora of China
Leaf type	Simple, compound	Flora of China
Leaf size	Maximum length of a leaf or leaflet (cm)	Flora of China

*For planting frequency and climatic suitability, the region is Europe (i.e. the area of the 15 European countries with planting data) when analysing establishment of 449 Chinese woody species in at least one of 15 European countries, while it is a given country when analysing establishment of the 38 species in multiple European countries.

We compiled data on 10 traits for each of the 449 species from the Flora of China (Wu *et al.*, 1994–2010): growth form (tree, shrub or liana), maximum height, earliest flowering month, flowering duration, earliest fruiting month, fruiting duration, sexual system (hermaphrodite, dioecious or monoecious), leaf retention (deciduous or evergreen), leaf type (simple or compound), leaf size (i.e. maximum length of a simple leaf or, for compound leaved species, of a leaflet) (Table 1). As the Flora of China did not report the height of lianas, we obtained data on maximum vertical height reached by lianas from Hortipedia (<http://en.hortipedia.com/>). These traits were chosen based on their availability and their potential ecological relevance. Maximum height is associated with competitive ability and seed dispersal distance (Pyšek *et al.*, 2009; Thomson *et al.*, 2011). Traits on flowering and fruiting phenology and sexual system are relevant for reproduction, and leaf traits reflect adaptations to seasonality and light capture (Pérez Harguindeguy *et al.*, 2013). Additionally, as a measure of native range size, we calculated for each species the proportion of 0.5° grid cells (c. 50 km × 50 km) in which the species occurs in China (Fang *et al.*, 2011), i.e. the number of grid cells in which it occurs divided by the total 4017 grid cells in China. We also considered including seed weight, but data were only available for 295 of the 449 species, and exploratory analyses indicated that seed weight did not explain much variation in establishment (results not shown). Therefore we did not further consider seed weight.

Bioclimatic niche-based modelling

We used BIOMOD, a niche based species distribution modelling platform (Thuiller *et al.*, 2009), to assess climatic suitability in Europe for the 449 species, on the basis of their native distribution in China. Details on the modelling procedure, as well as a validation of the use of Chinese distribution data only, are provided in Appendix S1. In short, we obtained grid cell based (0.5°) data on the occurrence of each species in China from an atlas of Chinese woody plants (Fang *et al.*, 2011). For both China and Europe, we extracted from WorldClim (<http://www.worldclim.org/>) a set of 19 bioclimatic variables that are derived from monthly temperature and precipitation values (Hijmans *et al.*, 2005) (Table S1 in Appendix S1). These variables reflect annual trends, seasonality and extremes that are known to determine plant distributions (Appendix S1). We first used BIOMOD to calibrate models by correlating the occurrences of each species in China with the 19 bioclimatic variables. We then projected the calibrated models onto Europe to assess climatic suitability for each species in each of the 1847 0.5° grid cells within the 15 European countries with planting data. Because we expected that a species would be able to establish in Europe as soon as the climate is suitable at any location, we used maximum instead of median or mean climatic suitability of each of the 449 species in Europe in the following analysis. This assumes that a species has been planted, or can disperse into, the climatically most suitable areas in Europe. We also ran the analysis with mean and median instead of maximum

climatic suitability, all three of which are highly correlated, but the fit of these models was slightly worse (Appendix S1). Similarly, for each of the 38 established species, we also assessed its maximum climatic suitability in each of the 15 European countries. We conducted bioclimatic niche based modelling with the R package 'biomod2' (Thuiller *et al.*, 2014).

Data analysis

To assess whether residence time, planting frequency, climatic suitability, native range size, species traits and their interactions explained establishment of the 449 species in Europe, we conducted two analyses. First, we analysed data on establishment in Europe for all species. Second, we analysed data on establishment in multiple countries for the subset of 38 species that have established in at least one country. Establishment in multiple countries could reflect multiple independent establishment events from separate plantings and/or spread of a species from one country to the other.

Establishment in Europe

We used generalized linear mixed effects models with a binomial error distribution to test whether establishment of the 449 species in Europe was linearly and, for continuous variables, also nonlinearly (i.e. quadratically) associated with residence time, planting frequency, climatic suitability, native range size, species traits and interactions between these variables. Because the number of explanatory variables (Table 1) was large relative to the number of observations ($n = 449$), we could not include all terms in a single model. Therefore, to avoid overfitting, we built a minimum adequate model largely by following Hosmer & Lemeshow (2004). First, we ran univariate models to test whether each variable was linearly and, for continuous variables, also nonlinearly associated with establishment. We centred each continuous variable on a mean of zero, and scaled it to a standard deviation of one. Second, to test whether the effects of variables interacted, we ran bivariate models for each possible pairwise combination of all the variables. However, because some of the classes of sexual system (dioecious, monoecious or hermaphrodite) did not contain all levels of the other variables, we could not fit interactions of sexual system. In both steps we used log likelihood ratio tests to assess the P value of each term by comparing models with and without the term.

We then ran a multivariate model that included all linear, nonlinear and interaction terms with $P < 0.1$ in the preceding two steps. We used, as is commonly done in other studies (e.g. Küster *et al.*, 2008), the less conservative threshold of $P < 0.1$ to ensure that we would not exclude variables that would be significant in a multivariate context. To find a minimum adequate model, we then removed one by one the interactions with $P \geq 0.05$, starting with the interaction with the highest P value. We

repeated this procedure until only interactions with $P < 0.05$ remained in the model. Next, to decide which of the main effects should be in the minimum adequate model, we first removed all the interactions from the model. We then removed nonlinear terms with $P \geq 0.05$ one by one, followed by linear terms. We repeated this whole process until we had a minimum adequate model in which all variables had linear, nonlinear or interaction terms with $P < 0.05$.

To assess a model's goodness of fit, we calculated the marginal R^2 of the minimum adequate model, indicating the variance explained by fixed factors (Nakagawa & Schielzeth, 2013). We also assessed the relative strength of association between establishment and each variable in the model by comparing the full model with the model without the variable. The difference in deviance between the two models indicates the amount of the variance explained by each variable, and thus yields a measure of the relative strength of the association (e.g. Kempel *et al.*, 2013). To ensure that our model had sufficient ability to produce reliable parameter estimates, we checked whether the number of events per explanatory variable was greater than five (Vittinghoff & McCulloch, 2007), and whether the variance inflation factor (indicating multicollinearity) was less than four (Zuur *et al.*, 2009). In all models, we accounted for phylogenetic non independence of the species by including family as a random factor. We also ran models with genus nested within family as random factors, but the output was similar (not shown). We conducted all analyses with R 2.3.2 (R Core Team, 2015), and ran generalized linear mixed effects models with the R package 'lme4' (Bates *et al.*, 2015).

Establishment in multiple countries

For the 38 species that have established in Europe, we further tested whether their establishment in multiple countries was associated with the same variables and interactions as used in the first analysis. We followed the same procedure as described above to build a minimum adequate model. The binary response variable was establishment of each species in each of the 15 countries. In other words, we had 15 observations for each species, one per country. Accordingly, we used country level instead of continent level estimates of planting frequency and climatic suitability. To account for non independence of observations of the same species in different countries, and of different species in the same country, we included species and country as random factors. We also ran models in which species was nested within genus and family, but the output was similar (not shown). Moreover, we tried to include random slopes for species and for country, but these models did not converge. We also did tests which showed that the results were not influenced by spatial autocorrelation (Appendix S3).

Table 2 Results of the minimum adequate model testing the linear effects of each explanatory variable, and the effects of interactions between the explanatory variables, on establishment of 449 Chinese woody species in at least one of 15 European countries.

	Variable or interaction	d.f.	χ^2	P	Percentage of variation explained*
Fixed	<i>Introduction history</i>				
	Residence time in Europe	1	20.92	<0.001	28.7
	Planting frequency in Europe	1	36.82	<0.001	54.2
	Climatic suitability in Europe	1	4.40	0.036	4.7
	<i>Species traits</i>				
	Fruiting duration	1	0.01	0.917	0.0
	Leaf retention	1	0.08	0.778	0.8
	<i>Interactions</i>				
	Leaf retention: residence time	1	4.25	0.039	6.1
Leaf retention: fruiting duration	1	3.96	0.047	5.5	
Random			Variance		
	Family		0.133		

The marginal R^2 (indicating the variance explained by fixed factors) of the model is 0.74.

*Based on the difference in deviance between the full model and a model without the variable.

RESULTS

Establishment in Europe

Descriptive statistics for the groups of established ($n = 38$) and non established ($n = 411$) species are given in Appendix S4. Of all variables with $P < 0.1$ in the univariate and bivariate models (Tables S7 & S8 in Appendix S5), the minimum adequate multivariate model (marginal $R^2 = 0.74$) retained residence time (relative percentage of variance explained 29%), planting frequency (54%), climatic suitability (5%) and two interactions – one between leaf retention and residence time (6%) and one between leaf retention and fruiting duration (6%) (Table 2). Probability of establishment significantly ($P < 0.05$) increased as residence time, planting frequency and climatic suitability increased (Table 2, Fig. 1a–c). None of the species traits had significant main effects on establishment, but some of the traits had significant interactions (Table 2). The increase in probability of establishment with residence time was stronger for evergreen than for deciduous species (Table 2, Fig. 1d). Moreover, for evergreen species, probability of establishment increased as fruiting duration increased, while the opposite was true for deciduous ones (Table 2, Fig. 1e).

Establishment in multiple countries

Eighteen species have established in more than one European country. Descriptive statistics for this group of 18 species and the group of 20 species established in only one country are given in Appendix S4. Of all variables with $P > 0.1$ in the univariate and bivariate models (Tables S7 & S8 in Appendix S5), the minimum adequate multivariate model (marginal $R^2 = 0.33$) retained planting frequency (relative percentage of variance explained 14%), linear (8%) and nonlinear (7%) terms for climatic suitability, flowering duration (17%), leaf type (19%) and two interactions – one between planting frequency and leaf type (10%) and one between climatic

suitability and fruiting duration (11%) (Table 3). Probability of establishment in multiple countries was positively associated with planting frequency and climatic suitability in these countries, but not with residence time in Europe (Table 3, Fig. 2a, b). Moreover, probability of establishment in multiple countries was nonlinearly associated with climatic suitability (Table 3, Fig. 2b): it increased with climatic suitability when the latter was >0.6 , but changed little or even decreased slightly with climatic suitability when the latter was ≤ 0.4 .

Of the 10 species traits, only flowering duration and leaf type were significantly associated with establishment in multiple countries (Table 3). Probability of establishment in multiple countries increased with flowering duration (Fig. 2c), and was higher for species with compound leaves than for species with simple leaves (Fig. 2d). Moreover, although for species with compound leaves the probability of establishment in multiple countries strongly increased with planting frequency, there was no such increase for species with simple leaves (Fig. 2e). Furthermore, the probability of establishment in multiple countries moderately increased with fruiting duration when climatic suitability was 0.85–0.9, but decreased as fruiting duration increased when climatic suitability was 0.1–0.6 (Fig. 2f).

DISCUSSION

Of the 449 introduced Chinese woody species, 38 have established in the wild in Europe. The extent of the distribution of the established species within each country and across ecosystems is not clear, but three of the species, *Ailanthus altissima*, *Buddleja davidii* and *Rosa rugosa*, are considered as invasive species in Europe. The relatively low rates of establishment (8.5%) and invasion (0.7%) are consistent with the tens rule of Williamson & Fitter (1996), according to which few of the introduced non native plant species establish and fewer become invasive.

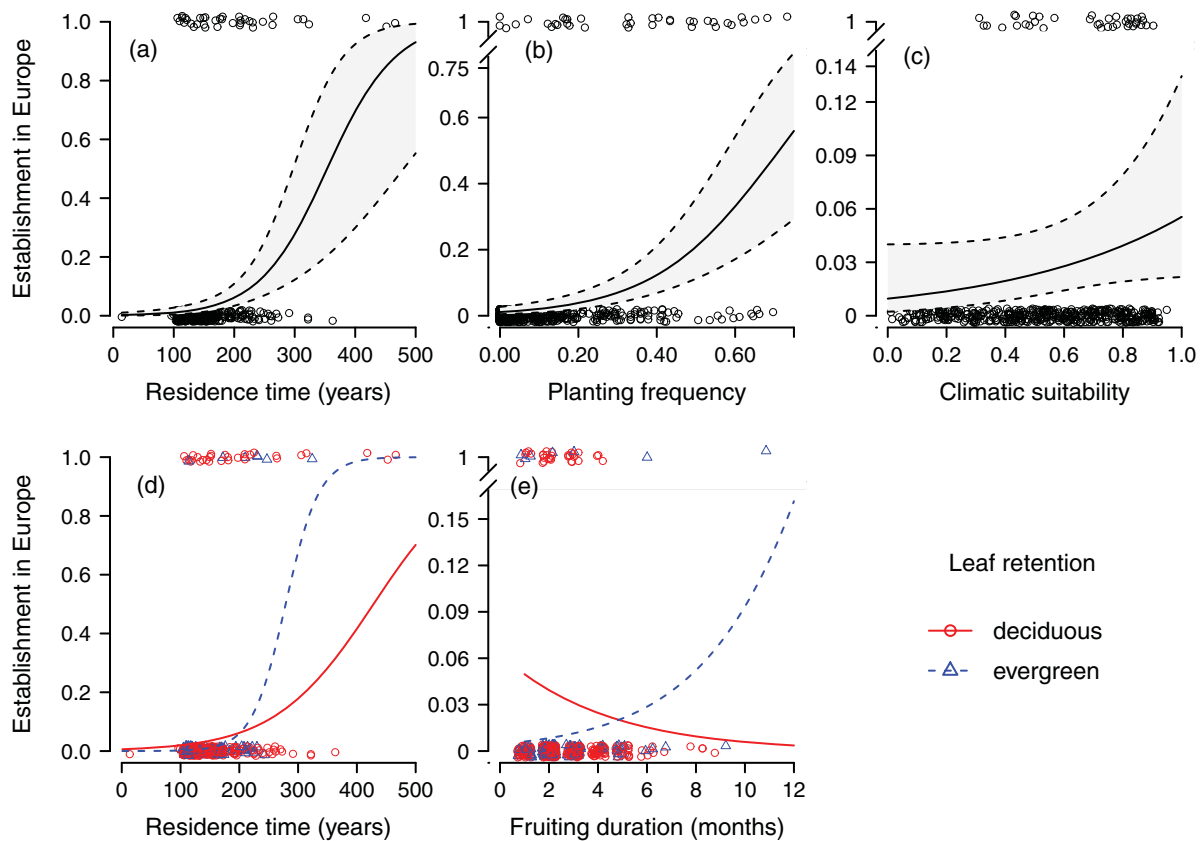


Figure 1 Probability of establishment, on the basis of the minimum adequate model, of 449 Chinese woody species in at least one of 15 European countries as a function of (a) residence time, (b) planting frequency, and (c) climatic suitability, and the interaction between (d) residence time and leaf retention and (e) fruiting duration and leaf retention. In (a) (c), the grey area between dashed lines indicates the 95% confidence interval. In (d) and (e), red circles and the red solid curve are for deciduous species, whereas blue triangles and the blue dashed curve are for evergreen species. Note that the *y* axis is truncated for parts (b), (c) and (e), and that to avoid that data points with the same value obscuring each other all data points have been slightly jittered.

Establishment in Europe was strongly and positively associated with residence time, planting frequency and climatic suitability. The latter two factors were also positively associated with establishment in multiple countries. The amount of variation in establishment explained by species traits, however, was low. Although establishment in Europe was not globally associated with any of the species traits, it was associated with leaf retention and fruiting duration via their interactions with residence time and leaf retention, respectively. Establishment in multiple countries was globally associated with a longer flowering duration and compound leaves, and it was associated with leaf type and fruiting duration via their interactions with planting frequency and climatic suitability, respectively. Our study is among the first (see also Küster *et al.*, 2008) to empirically show that the association between some species traits and establishment of non native plants is context dependent.

Residence time and planting frequency

A longer residence time provides species with more time to accumulate and release propagules, and to disperse in a region. Therefore, a longer residence time may increase a

species' chance to establish self sustaining populations in the wild (Richardson & Pyšek, 2012). We indeed found that establishment was positively associated with residence time (established and non established species had mean residence times of 209 and 148 years, respectively; Appendix S4). This implies that, with time, some of the currently non established species will establish. Residence time, however, was not associated with establishment in multiple countries. This might be because our single value of residence time for Europe does not reflect variation in residence time of a species across countries.

All woody species in our data have been planted as ornamentals. A higher planting frequency in gardens may increase propagule pressure and establishment (Pyšek *et al.*, 2009). In line with this, the planting frequency of established species was three times greater than that of non established species (Appendix S4), and explained more variation in establishment than all other factors together (Table 2). The positive association between planting frequency and establishment in Europe, as well as in multiple countries, could also partly reflect that species might be planted more frequently in an area with a suitable climate. However, for the 449 species, the

Table 3 Results of the minimum adequate model testing the linear and, for continuous variables, also nonlinear (i.e. quadratic) effects of each explanatory variable, and the effects of interactions between the explanatory variables, on establishment of the 38 species in multiple countries

	Variable or interaction	d.f.	χ^2	<i>P</i>	Percentage of variation explained*	
Fixed	<i>Introduction history</i>					
		Planting frequency in a country	1	76.83	0.009	14.1
		Climatic suitability in a country	1	5.29	0.021	7.7
		(Climatic suitability in a country) ²	1	4.13	0.042	7.3
	<i>Species traits</i>					
		Flowering duration	1	5.25	0.021	16.9
		Fruiting duration	1	1.68	0.194	6.0
		Leaf type	1	8.91	0.003	19.3
	<i>Interactions</i>					
		Planting frequency: Leaf type	1	75.61	0.018	10.3
	Climatic suitability: Fruiting duration	1	6.10	0.014	11.2	
	Variance					
Random	Species		0.134			
	Country		1.586			

The marginal R^2 (indicating the variance explained by fixed factors) of the model is 0.33.

*Based on the difference in deviance between the full model and a model without the variable.

correlation between planting frequency and climatic suitability in Europe was weak and non significant ($r = 0.08$, $P = 0.076$, $n = 449$). So was the correlation between planting frequency and climatic suitability in multiple countries ($r = 0.03$, $P = 0.42$, $n = 570$), for the 38 established species. Among the established species, the average planting frequency of the three highly invasive species, *A. altissima*, *B. davidii* and *R. rugosa*, was much higher than that of other species (0.67 vs. 0.40, respectively). Many other studies have also shown that increases in planting frequency are associated with increases in local and regional establishment of non native woody species (e.g. Bucharova & van Kleunen, 2009; Pyšek *et al.*, 2009).

Planting frequency could partly be confounded with residence time, because the longer a species has been present in cultivation, the more likely it is to have been planted widely (Richardson & Pyšek, 2012). In our study, the correlation between planting frequency and residence time among all species was significant but weak ($r = 0.20$, $P < 0.001$), and among the 38 established species it was not significant ($r = 0.20$, $P = 0.24$). As establishment in Europe was positively associated with both residence time and planting frequency after holding the other constant, the association between planting frequency and establishment is unlikely to be a spurious one.

Climatic suitability

Climate determines whether a species can germinate, grow, survive and reproduce, and therefore is expected to be a major determinant of the potential geographical distribution of non native plants (Thuiller *et al.*, 2005). We indeed found that climatic suitability was associated with establishment in

Europe. Given that we tested many variables, and the P value (0.036) was just below 0.05, we cannot exclude that the climatic suitability effect is a Type I error (e.g. Moran, 2003). However, the observed association of establishment with climatic suitability is in line with the findings of many other studies on the importance of climatic suitability in plant invasions (Thuiller *et al.*, 2005; Petitpierre *et al.*, 2012). Furthermore, climatic suitability was also positively associated with establishment in multiple countries, although only so in the range of intermediate to high climatic suitability (Fig. 2b). Despite the fact that the quadratic component of climatic suitability had a P value just below 0.05 (0.042), it illustrates that associations may be nonlinear (van Kleunen *et al.*, 2015b).

Some species have established (e.g. *Gleditsia triacanthos*) or become invasive (e.g. *R. rugosa*) in areas with low or intermediate climate suitability (Figs 1c & 2b, f). This may indicate that the climatic niches of these species were not fully captured by their distribution in China. Possible causes are that they may be native to other countries as well (see Appendix S1) and that the spatial resolution of 0.5° grid cells was too coarse to capture the true climatic niches of some species. Alternatively, climatic niches may have shifted after the introduction of the species to Europe (Broennimann *et al.*, 2007). Moreover, other environmental factors such as soil type and resource availability (Theoharides & Dukes, 2007), which were not considered in our study, are likely to also affect establishment. Nevertheless, the overall positive effect of climatic suitability indicates that, for a majority of our species, climatic niches are conserved between the native and new ranges (Petitpierre *et al.*, 2012).

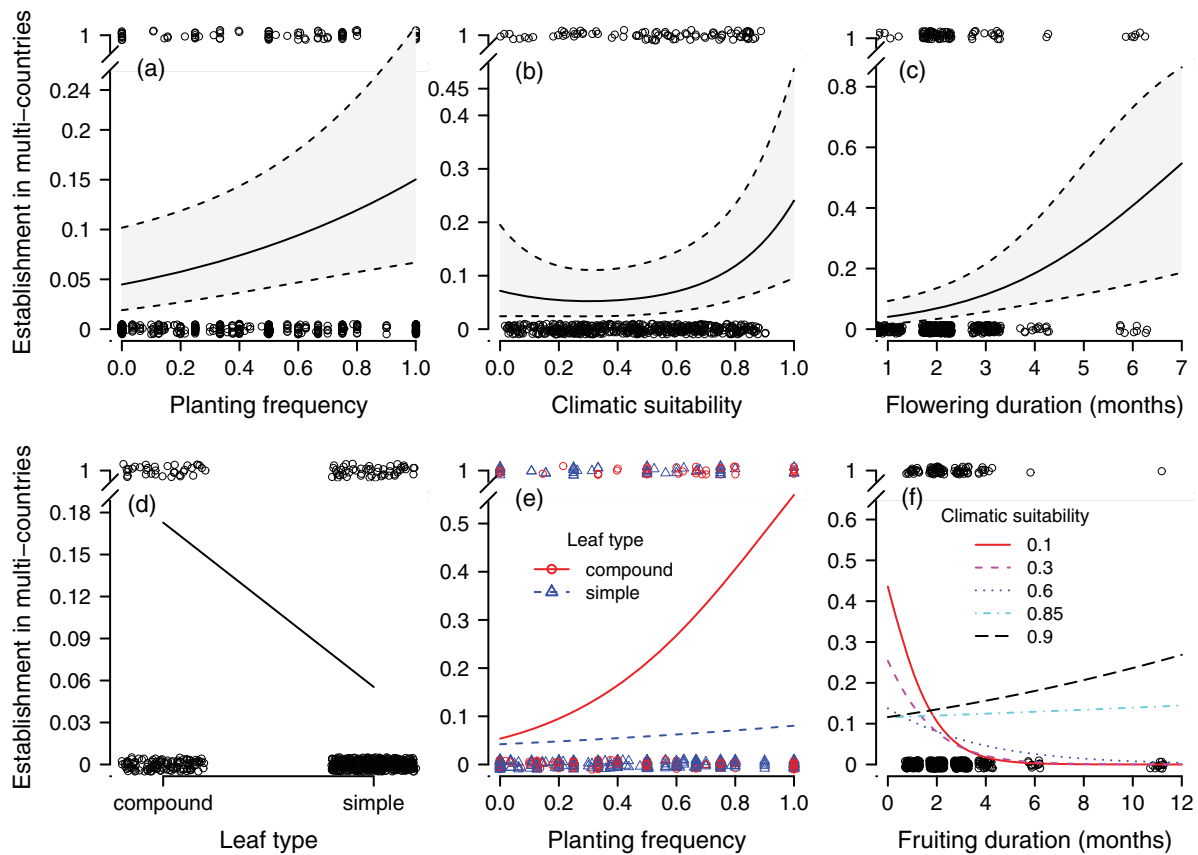


Figure 2 Probability of establishment, on the basis of the minimum adequate model, of the 38 species in multiple countries as a function of (a) planting frequency, (b) climatic suitability, (c) flowering duration, and (d) leaf type, and the interaction between (e) planting frequency and leaf type and (f) climatic suitability and fruiting duration. In (a) (c), the grey area between dashed lines indicates the 95% confidence interval. In (e), red circles and the red solid curve are for compound leaved species, whereas blue triangles and the blue dashed curve are for simple leaved species. Note that the y axes are truncated, and that to avoid data points with the same values obscuring each other all data points have been slightly jittered.

Species traits and their interactions

Few if any species traits have been reported to be universally associated with the success of non native plants (Daehler, 2003; Pyšek & Richardson, 2007; van Kleunen *et al.*, 2010). Therefore, it has frequently been suggested that the effects of traits are context dependent (Daehler, 2003; Moles *et al.*, 2008; Pyšek *et al.*, 2009; Richardson & Pyšek, 2012; Leffler *et al.*, 2014; van Kleunen *et al.*, 2015b). None of the traits we characterized was, as a main effect, significantly associated with establishment in Europe, but the interactions of leaf retention with residence time and with fruiting duration were. However, given that we tested for many different effects, and the P values of the two interactions (0.039 and 0.047) were only just below the 0.05 significance level, we cannot exclude that these significant interactions are Type I errors (e.g. Moran, 2003). Therefore these interactions should be interpreted cautiously.

Although the 335 deciduous and 114 (88 angiosperms, 26 gymnosperms) evergreen species in our study differed neither in residence time (t 0.201, d.f. 245, P 0.841) nor in establishment (Table 2), evergreens required on average less

time to establish than deciduous species. The reasons could be that evergreens have shorter generation times and more defensive compounds (to deal with novel conditions) than deciduous species (Smith, 1993). Although evergreen and deciduous species also had comparable fruiting durations (2.67 vs. 2.61 months, respectively), establishment probability was greater for the evergreens with a longer fruiting duration (e.g. *Ligustrum lucidum*), while the opposite was true for deciduous species with a similarly long fruiting duration (e.g. *Rhododendron yunnanense*) (Fig. 1e). Species that can produce fruits during most of the year are more likely to produce some seeds during periods that are optimal for dispersal or germination. While evergreen species, which are able to grow and support seed development during most of the year, can benefit from longer fruiting periods, deciduous species, which have a limited annual growth period, might not.

A longer flowering period was positively associated with establishment in multiple countries. This association is consistent with the results of other studies (Küster *et al.*, 2008; Chrobok *et al.*, 2013; Gallagher *et al.*, 2015), and might

reflect that a long flowering period allows plants to allocate more resources to reproduction. Moreover, for animal pollinated plants, a long flowering period increases the likelihood that the flowering period will overlap with the activity of pollinators.

Plant phenology is highly responsive to seasonal and annual climatic variations (Cleland *et al.*, 2007). We found that the association between establishment in multiple countries and fruiting duration shifted from moderately positive to negative as climatic suitability decreased (Fig. 2f). A possible explanation is that when the climate is highly suitable (0.85–0.9), an increase in the fruiting period results in an increase in reproduction. However, when the climate is less suitable, fruiting during a narrow time window with suitable temperature and water availability might be more advantageous.

Little is known about the advantages and disadvantages of having compound leaves. It has been hypothesized that, compared with species with simple leaves, species with compound leaves might be better adapted to seasonal droughts (Givnish, 1979). Drought periods are common in many regions of Europe (Spinoni *et al.*, 2016) and might thus have promoted establishment in multiple countries. It has also been suggested that compound leaves are an adaptation that allow rapid growth under favourable light conditions (Givnish, 1979; Malhado *et al.*, 2010). Given that most of the natural vegetation in Europe has been highly disturbed (Millennium Ecosystem Assessment 2005, <http://www.millenniumassessment.org/>), species with compound leaves might have taken more advantage of the high light conditions in these areas. However, as indicated by the significant interaction between leaf type and planting frequency, high planting frequency is a prerequisite for the increase in establishment probability of species with compound leaves. In other words, if a non native plant is rarely planted, it is unlikely to establish irrespective of whether it has compound or simple leaves. Again, this emphasizes that the role of traits in the success of non native plants is dependent on other factors.

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SUPPORTING INFORMATION

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Appendix S1 Bioclimatic niche based modelling.

Appendix S2 Locations of European gardens.

Appendix S3 Results of the analysis accounting for spatial autocorrelation.

Appendix S4 Descriptive statistics for the groups of species.

Appendix S5 Results of univariate and bivariate models.

Table S1 List of the 19 bioclimatic variables used in bioclimatic niche based modelling to assess climatic suitability.

Table S2 Comparison of the importance of maximum, mean and median climatic suitability in explaining establishment success of 449 Chinese woody species in Europe, and establishment of 38 woody species in multiple countries.

Table S3 Results of the minimum adequate model testing the linear and, for continuous variables, also nonlinear (i.e. quadratic) effects of each explanatory variable, and the effects of interactions between the explanatory variables, on establishment success of the 38 species in multiple European countries.

Table S4 Results of generalized linear mixed effects models accounting for spatial autocorrelation, testing the linear and, for continuous variables, nonlinear (i.e. quadratic) effects of each explanatory variable (univariate models), on establishment of the 38 species in multiple European countries.

Table S5 Results of generalized linear mixed effects models accounting for spatial autocorrelation, testing the effects of interactions between all possible pairwise combinations of the explanatory variables except sexual system (bivariate

models) on establishment of the 38 species in multiple European countries.

Table S6 Descriptive statistics for the 449 species introduced to Europe, according to whether they are established in at least one of the 15 European countries or not, and for the 38 species established in Europe, according to whether they are established in more than one country or not.

Table S7 Results of generalized linear mixed effects models testing the linear and, for continuous variables, nonlinear (i.e. quadratic) effects of each explanatory variable (univariate models), on establishment of 449 Chinese woody species in at least one of 15 European countries (i.e. in Europe) and on establishment of the 38 species in multiple European countries.

Table S8 Results of generalized linear mixed effects models testing the effects of two way interactions between all possible pairwise combinations of the explanatory variables (bivariate models) on establishment of 449 Chinese woody species in at least one of 15 European countries (i.e. in Europe) and on establishment of the 38 species in multiple European countries.

Figure S1 Principal component analysis of 19 bioclimatic variables in China, Europe and Asian countries other than China.

Figure S2 Correlations between maximum climatic suitability, median climatic suitability and mean climatic suitability for the 449 species in Europe and the 38 established species in each of the 15 European countries.

Figure S3 Location of the 198 gardens (botanical gardens, arboretums, and castle, public and private parks) in the 15 European countries included in our dataset.