

RESEARCH ARTICLE

Invasion success and impacts depend on different characteristics in non-native plants

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Abstract

Aim: Biological invasions threaten biodiversity globally. Large-scale studies of non-native plant species invasiveness typically focus on identifying ecological differences between naturalized and invasive species that account for their spread from sites of initial establishment (i.e., invasion success). However, invasive species differ widely in the magnitude of their impacts, suggesting the characteristics that favour invasion success might not necessarily predict the consequences of that invasion. Here we test whether those factors that increase the probability of plant species invasion also explain the severity of impacts.

Location: China.

Methods: We compiled a database of the invasiveness, biogeographic origins, life history traits, and introduction history for 538 non-native plants in China and modelled differences in (a) naturalized and invasive species; (b) the spatial extent of invasion; and, (c) the severity of invasion impacts among successful invaders.

Results: Invasion success and the spatial extent of invasion shared similar influencing factors. However, these clearly differed from the predictors of severe invasion impacts. Unintentionally introduced non-native plants with shorter life cycles and longer residence times were more likely to become invasive and to invade a larger area, while taller plants introduced from the Americas tended to have more severe impacts on the native ecosystems of China.

Main Conclusions: These results illustrate the different roles of introduction history, biogeographical origin and biological traits in determining the invasion success and spatial extent of invasion versus the severity of invasive species impacts. We suggest that factors associated with evolutionary adaptation and population expansion might determine invasion success and extent, while traits related to the relative competitive ability of invasive species determine the severity of impacts. Identifying specific characteristics of species that distinguish among successful invaders most likely to result in more severe impacts could help with planning more effective interventions.

KEYWORDS

biological traits, introduction history, invasion impacts, invasive plants, invasiveness, naturalized plants, species comparisons

1 | INTRODUCTION

In an ever-more connected world, countries struggle to manage the risks associated with biological invasion. Invasions are already among the most threatening mechanisms of global change (Carboni et al., 2016), producing changes in community composition and ecosystem structure and functioning (Levine et al., 2003). Yet, not every naturalized species will spread from its locations of establishment in ways that define a species as invasive ('invasion success', Hamilton et al., 2005) and the magnitude of invasion impacts differs greatly among those species which do become invasive (Blackburn et al., 2014; Pyšek et al., 2012). Identifying the determinants of both invasion success and of any resulting impacts can help clarify the underlying mechanisms and provide information useful for the prioritization of species in invasion management (Colautti et al., 2014). Given that underlying ecological processes drive differences between invasion success and impacts (MacDougall et al., 2009), it is perhaps unlikely that the same characteristics which make a species invasive also determine the resulting invasion impacts. To date, however, studies that simultaneously consider the determinants of invasion success and impacts over spatial scales relevant to the management of biological invasion have been lacking.

Factors contributing to the performance of non-native plants (so-called 'invasiveness') include their biological traits, biogeographical origin and introduction history (van Kleunen et al., 2010). There might be other factors that could also influence invasiveness, but these three factors are well examined and their contributions well established. Since Baker (1965) introduced the concept of "ideal weeds" – where certain traits gave rise to variations in the invasiveness of non-native plants – many studies have attempted to determine the relationship between biological traits and plant invasiveness (Leishman et al., 2007). Traits correlated with invasiveness have included relative growth rate (Leishman et al., 2007), seed mass (Carboni et al., 2016), maximum height, and plasticity. Plants with shorter life history usually have higher reproduction rates and may be able to evolve more quickly to adapt to new environments, thus improving invasion success (Pyšek & Richardson, 2007). Flowering phenology is important for plant fecundity, and non-native plants with earlier and longer flowering time can have greater impacts in invaded sites (Alexander & Levine, 2019). Plant seed mass is generally positively associated with seedling size and survival (Moles, 2018), and thus may influence plant seedling competitive ability. Plant maximum height could determine the ability of intercepting light in competition with neighbouring individuals (Kunstler et al., 2015), such that it may be positively related to the impact severity of non-native species. Mating system is also important for plant reproduction success, especially for early-stage invasions, because it could decrease

pollination in small-population dioecious plants. However, despite these well understood general principles, a consensus view on the most important traits has proven elusive (Pyšek & Richardson, 2007).

The unique evolutionary history and biogeographical specifics of different species influence both their intrinsic features as invasive plants and the strength of their interactions with native biota. This in turn affects the ability of non-native species to occupy empty environmental niches (Shea & Chesson, 2002) or escape from specialized enemies (van Kleunen et al., 2015). Introduction history also plays an important role in determining the invasiveness of species, with the key components including (Simberloff, 2009): residence time (time since introduction), the pathway by which it was introduced to the new habitat (particularly whether this was intentional or unintentional) and the propagule pressure associated with the introduction. Generally, longer residence times and higher propagule pressures contribute to population expansion, habitat adaptation and the spread of non-native species (Lockwood et al., 2005).

While predicting invasiveness clearly involves consideration of many potentially interacting factors, understanding their relative importance is of value because it allows species to be prioritized for effective intervention. Comparing the characteristics of non-native species that differ in their invasiveness is one approach to this problem (van Kleunen et al., 2010). As naturalization and invasion are distinct stages during the invasion process (Blackburn et al., 2011; Richardson et al., 2000), a widely used method is to compare the characteristics of naturalized species (non-native species that have established sustainable populations but not spread from their sites of introduction) with species recognized as having become invasive (Richardson et al., 2000). To spread from its introduction sites, naturalized plants may face multiple barriers, such as small population size, low genetic diversity, lack of effective dispersal, and maladaptation to new environments (Blackburn et al., 2011). There usually exists a long 'lag phase' after establishment, and only a subset of naturalized species will overcome these barriers and spread, thus becoming invasive (Aikio et al., 2010). Therefore, comparing naturalized plants with invasive plants could help us understand what characteristics of naturalized plants place them at an advantage of adapting to new environments, increasing their dispersal and becoming invasive. In the first such naturalized-invasive comparative study, Williamson and Fitter (1996) found plant size and propagule pressure were significantly correlated with invasion success in Britain. Subsequently, the method has been applied in several regions, including the conterminous United States (Sutherland, 2004), Puerto Rico and the Virgin Islands (Rojas-Sandoval & Acevedo-Rodríguez, 2015).

Although this approach has proven useful for identifying the factors determining invasion success, it neglects the magnitude of invasion impacts. As these impacts can vary in both their extent and

in their intensity (Nentwig et al., 2016), this suggests there are two distinct dimensions to be considered. By definition, invasion success requires some degree of spread from the point of introduction, yet the spatial extent of invasion (hereafter invasion extent) can differ greatly among invasive species and could depend on specific factors. For example, residence time and nitrogen-fixation were associated with a greater spatial extent in South Africa (Wilson et al., 2007). Second, invasive species can vary in the severity of impacts they produce in invaded ecosystems (depending on species local abundance and per-capita impact) and recent theoretical and empirical studies have begun to focus on these variations (Evans et al., 2018; Li et al., 2018; Pyšek et al., 2012). For example, Li et al. (2018) found experimental support for MacDougall et al.'s (2009) prediction that invasive species with greater fitness advantages and lower niche differences relative to native species would exhibit more severe impacts to their invaded communities in a study of invasive microorganisms.

To date, no regional or continental scale studies have sought to determine the relative importance of biological traits, biogeographical origin and introduction history on invasion success, invasion extent and impact severity. Such an approach could help identify whether specific characteristics are associated with each of these stages of invasion. Because invasion success and extent are both associated with spread, it is reasonable to expect that at least some of the characteristics of species will overlap. However, it is less clear whether these will also be associated with severity of impacts, or whether different characteristics are involved. If it is the latter, this could have important implications for how potentially invasive species should be prioritized for management.

In this study, we adopt a two-stage approach to analyse the characteristics influencing invasion success and impacts of non-native plants in China. Our aims were to first determine which factors explain the probability that a naturalized plant may become invasive. Then, for those plant species that have become invasive, to determine which factors best explain the spatial extent and severity of invasion impacts they create (Figure 1). Comparing the results for these two phases of the investigation then answers the question of whether a common set of characteristics are involved in creating

both an increased likelihood of invasion and more severe consequences in terms of invasion extent or severity of impacts. We hypothesized that (a) both invasion success and spatial extent in plants will depend on similar characteristics, specifically those which increase their rate of spread and adaptive ability in new environments (e.g., shorter life history); while, (b) impact severity will depend more on characteristics associated with competitive ability in biotic interactions between non-native species and native species. In other words, we expect the factors affecting the impact severity of invasive species will differ from those associated with invasion success.

2 | MATERIALS AND METHODS

Our study extent was China, for which we compiled a database of the taxonomy, invasiveness, biological traits, biogeographic origin, global naturalization range size and introduction history of non-native plants (Table 1).

2.1 | Invasion success and impacts of non-native plant species

As is common for regional-scale comparative studies (e.g., Milbau & Stout, 2008), we defined invasion success as whether non-native naturalized species have successfully spread from sites of initial establishment and become invasive (Richardson et al., 2000). We used the most recent and comprehensive inventory of naturalized plants in China, the checklist compiled by Jiang et al. (2011). We first excluded invasive and native species mistakenly reported in this inventory based on review of the same primary sources, the flora of China and checklists of invasive plants (Ma, 2014; Ma et al., 2013). We also ignored taxonomic varieties to provide consistent taxonomic resolution. We retained 272 naturalized plant species in the first stage of analysis for modelling invasion success.

For the taxonomy and invasion impacts of invasive plants, we broadly followed the checklist of invasive plants from Ma et al. (2013)

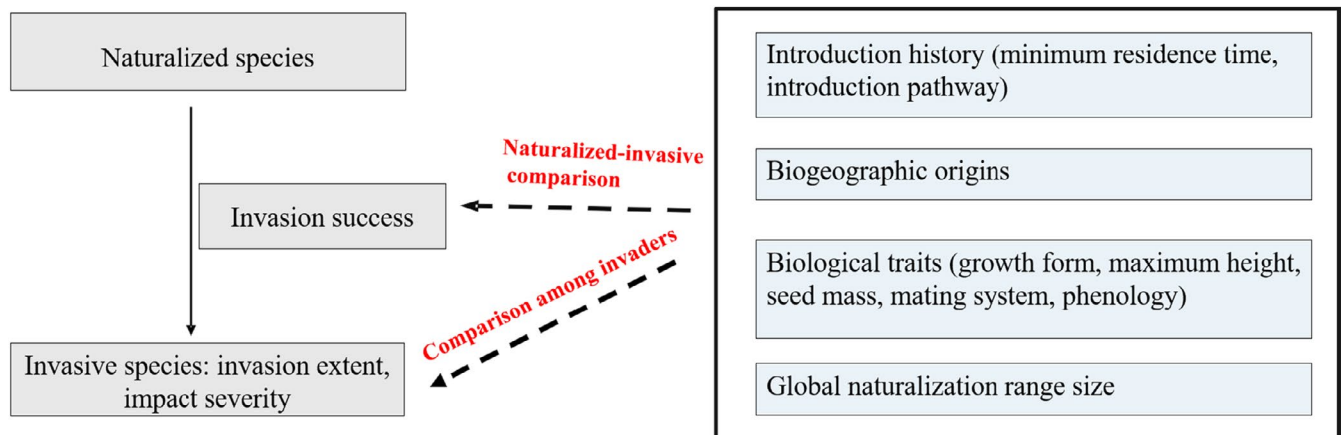


FIGURE 1 Conceptual framework of this study. Comparisons between naturalized plants and invasive plants and comparisons among invasive plants were used to investigate the invasion success and invasion impacts, respectively

TABLE 1 List of species attributes analysed in the study

Type and attributes	Levels
Biological traits	
Growth form (538)	Annual herb (A), biennial herb (B), perennial herb (P), shrub (S), tree (T), vine (V), liana (L)
Seed mass (342)	Thousand seed weight (g)
Flowering time (477)	Month
Flowering starting time (477)	Month
Mating system (538)	Bisexual (B), dioecious (D), monoecious (M), polygamous (P)
Maximum height (490)	Meter (m)
Introduction history	
Introduction pathway (537)	Intentional introduction (I), unintentional introduction (U)
Minimum residence time (514)	Year
Biogeographical origin	
Origin (537)	Africa (A), Temperate Asia and Europe (E), Central and South America (C), North America (N), Oceania (O), Tropical Asia (T), the Americas (NC, distributed in both North America and Central and South America)
Performance worldwide	
Global naturalization range size (531)	The number of naturalized regions

and Ma (2014), which represent the most comprehensive and current information on the impacts of invasive plants in China. These studies rank 268 invasive plant species according to their environmental impact (<http://www.iplant.cn/ias/protlist?page=9>; in Chinese). Environmental impacts of invaded ecosystems included those defined at the level of individual species (e.g., population decline or local extinction of one or more native species); communities (e.g., changes in structure or composition); or on ecosystem functioning (e.g., changes in nutrient cycling or primary productivity) (Levine et al., 2003).

For each invasive species, Ma et al. (2013) and Ma (2014) assigned an ordinal impact rank based on review of published invasion reports. Impact rankings were essentially based on two criteria. First, the species had to be associated with a severe environmental impact (e.g., significant versus non-significant changes in the invaded ecosystems). Species having a demonstrated severe environmental impact were then further classified according to the spatial extent of their invasions. Ranks 1 and 2 species both had severe impacts over multiple biogeographical regions, while rank 3 species produced severe impacts only within a single biogeographical region. Species assigned to Rank 4 could have any spatial extent of invasion but were not associated with any significant environmental impacts. As with other studies ranking invasion impact, such as the generic impact scoring system (GISS, Nentwig et al., 2016) and Blackburn et al. (2014), the ranking system used in Ma et al. (2013) and Ma (2014) was derived from published evidence. Species lacking sufficient information were excluded from ranking and classified as not having adequate data. Although Ma (2014) specifies the different categories of environmental impacts, because of data limitations, neither Ma et al. (2013) nor Ma (2014) provided a separate ranking

for species within each of these categories as has sometimes been possible (e.g., Evans et al., 2018; Nentwig et al., 2016).

Rather than adopting the single ordinal impact classification of Ma et al. (2013) and Ma (2014), we separately analysed the factors that determined whether an invasive species resulted in severe impacts and the spatial extent over which those impacts occurred. While both invasion success and spatial extent of invasion involve spread, a species could spread extensively from a single point of origin over a narrow range in conditions (e.g., within one or two adjoining counties), yet not have a distribution that extends over regional scales (e.g., to counties with widely different physiographic conditions). Conversely, a naturalized species could occur in many counties (perhaps because of widespread intentional introductions for agricultural or horticultural use), but never become invasive. Understanding the characteristics of a species that would enable it to become invasive over a large spatial extent given the range of environmental variations in mainland China is not only important for understanding invasion but is also of intrinsic biogeographical interest (Gaston, 2003; Ricklefs et al., 2008).

To create our two invasion impact response variables, we assigned all species classified by Ma et al. (2013) and Ma (2014) with ranks 1–3 ($n = 187$) as imposing a severe impact on invaded ecosystems and those with rank 4 ($n = 79$) as having non-significant or negligible impacts on invaded ecosystems. Thus, we adopted a binary impact severity classification, thematically following Pyšek et al. (2012). We calculated spatial extent of invasion independently of the Ma et al. (2013) and Ma (2014) rankings, quantifying this as the number of counties invaded by each species identified as having created a severe impact. To do this we used the species distribution records in the Chinese Vascular Plant Distribution Database (<http://www.cvh.ac.cn/>), which includes more

than six million specimen records with the majority of these georeferenced to at least county level (China contains 2,377 counties in total, with a mean size of 4,238 km²). We used the integer number of counties invaded according to the database as our estimate of the spatial extent of invasion impacts.

2.2 | Plant characteristics

For plant characteristics, we chose the traits that could play key roles in determining plant performance outside a species native range (such as environmental adaptation, competitiveness and fecundity; refer Table 1). Information on growth forms, maximum height, flowering phenology and mating systems were obtained from *Flora of China* (Flora of China Editorial Committee, 1993). Flowering time was measured as the difference between the mean onset and cessation of flowering. For prostrate creeping plants, maximum height was set to zero. Seed mass data were retrieved from the Kew Garden Seed Information Database (<https://data.kew.org/sid/>); for species with more than a single record, we used the mean value.

Minimum residence time for each species was estimated based on its first reported time in the literature and/or the collection date for the first herbarium specimen present in the Chinese Virtual Herbarium (<http://www.cvh.org.cn/>), whichever date was earlier. The origins and introduction pathways of non-native species were obtained from Jiang et al. (2011) and *The Survey Reports on Chinese Alien Invasive Plants* (Ma, 2014). Origin classifications were based on the Biodiversity Information Standards (TDWG, <http://www.tdwg.org>) and because the database does not distinguish between European and temperate Asian origin for most species, we pooled these regions. Introduction pathway was categorized as 'unintentional' or 'intentional' introduction (e.g., introduced crops, pastures, medicinal plants, horticultural plants).

Our database also included the global naturalization range size of non-native species as it has been demonstrated that species' invasive performance worldwide can be an effective predictor for invasiveness in a specific region (Pyšek et al., 2012). Global naturalization range size was measured as the number of regions that species had colonized worldwide according to the GloNAF database (van Kleunen et al., 2019). To avoid circularity, we removed the regions in China within the GloNAF database as these overlapped with the measure of invasion extent. Explanatory variables used in modelling are summarized in Table 1.

2.3 | Data analyses

We built individual regression models of (a) invasion success: whether an introduced species was likely to become invasive (b) invasion extent: the spatial extent of invasive species, and, (c) impact severity: whether invasive species created a severe impacts (independent of the extent of their invasion). Binary responses were invasion success (successful invaders = 1, naturalized but not invasive = 0) and impact severity (severe-impact = 1, mild-impact = 0). Invasion extent

was a count variable (integer number of counties invaded). All models used a common set of predictors (Table 1), including six continuous variables (minimum residence time, seed mass, maximum height, flowering start time, flowering time and global naturalization range size), three categorical variables (growth form, mating system and biogeographic origin) and one binary variable (introduction pathway, unintentional vs. intentional). Prior to modelling, all numeric explanatory variables were $\log(x + 1)$ transformed. For any missing values for continuous predictors in our database, we used multivariate imputation by chained equations based on the relationships between continuous traits to estimate values, using the 'mice' package for R (van Buuren & Groothuis-Oudshoorn, 2011).

We used both boosted regression trees (BRT) to do determine the most important explanatory variables for each invasion response. Rather than fitting a single model of best fit as occurs with standard regression, BRT is an ensemble method, combining regression trees (relating explanatory variables to the response through recursive binary splits) with boosting, where the overall tree is built by combining many simple models to give improved and robust predictive performance. BRT brings the important advantages of tree-based methods, handling different types of explanatory variables, being able to fit complex non-linear relationships and in automatically detecting interaction effects between explanatory variables (Elith et al., 2008).

The invasion success BRT model was fit using a learning rate of 0.005 and a tree complexity of 5. The impact severity model and invasion extent models were fitted using a learning rate of 0.005 and a tree complexity of 7 (to account for the reduced degrees of freedom due to modelling only successful invading species). The optimal number of trees for each model was determined based on ten-fold cross validation: 600 trees for invasion success, 350 trees for invasion extent and 250 trees for impact severity. We evaluated the goodness of fit of each model by calculating the pseudo R^2 of fitted values against observed values. We also extracted the relative importance values of selected explanatory variables in each model. Variable relative importance is calculated based on the number of times the variable was selected for splitting in the models, which is an indication of the proportion of variation it explained in the final BRT model (Elith et al., 2008). To visualize the relationship between each explanatory variable and invasion success and impacts, we used partial response curves (also known as partial dependence plots), which calculate the effect of a variable on the response after accounting for the average effects of all other variables in the model (Elith et al., 2008). As partial response curves do not perfectly capture the response to an explanatory variable in the presence of strong interactions or highly correlated explanatory variables (Elith et al., 2008), we tested for pairwise interactions in each model. We present partial response curves for the most important explanatory variables in the main text and other explanatory variables are shown in Appendix S1.

To add greater context and test the generality of the BRT result, we also fit generalized linear models (GLM) using a binomial error structure and logit link function for invasion success and impact severity and negative binomial errors and log link for the integer spatial extent response. While we lacked a full phylogenetic tree, we did test

for sensitivity of invasion success and impacts to phylogenetic relatedness by comparing the GLM with standard error structure, with a phylogenetic mixed model (incorporating a nested random effect for order and class). As this did not qualitatively affect results, we focus on the GLM with standard error structure. Similarly, as the BRT and GLM models produced qualitatively similar results, we focus on the results of the BRT in the main text because of its superior predictive performance. However, for additional context on the nature of the responses we refer to both the BRT and GLM results and refer readers to the Supporting Information for detail on the latter (Appendix S3).

We inferred the role of each explanatory variable in determining invasion success, invasion extent and impact severity by comparing both the identity and relative importance of explanatory variable within each final BRT model. If model selection results in different combinations of explanatory variables, or their effect changes sign, this implies a difference in the effect of the explanatory variable on the invasion response of interest. However, as relative importance alone does not reflect the nature of the responses of invasiveness (e.g., positive, negative, unimodal), we also compared the partial response curves of the four most important variables in each of the three models and compared these with the GLM coefficient sign and magnitude. Comparison of the partial response curves for the same explanatory variable in different models then provides a qualitative test of any differential effect on the stages of invasion, while revealing more about the nature of their underlying effects. We also show the fitted values of invasion success and impacts in relation to each of the explanatory variables were shown in Appendix S2 (Figure S2.1–2.3, Supporting Information).

As the selection of each explanatory variable within the regression trees is effectively a hypothesis test, we inferred support for our main questions based on the final explanatory variables in each model and their relative importance. Where models select the same explanatory variable, this implies the response shares the same determinants. However, to further elaborate on the extent to which the same factors influenced invasion success and invasion impacts (invasion extent and impact severity), we did two sets of post hoc analyses. First, we calculated Pearson correlations of variable relative importance between the three models. Higher correlation indicates increased similarity in model results in terms of the relative importance of variables. Second, we separately compared the modelled probability of invasion success with (a) their observed invasion extent, and (b) their impact severity. If the fitted probability of invasion success was positively associated with either of these invasion impacts, this would support a conclusion that the outcomes could have similarly dependencies. To test for a relationship between the probability of success and spatial extent (two continuous outcomes) we used a general linear model (log transforming spatial extent due to left-skewed distribution), and to test for a difference in the mean probability of success in mild and severe-impact invasive species (continuous and categorical outcomes) we used a Student's *t*-test. All analyses described above were performed with R (R Development Core Team, Version 3.3.0, 2016), with boosted regression trees modelled using the R package 'dismo' (Elith et al., 2008).

3 | RESULTS

3.1 | Factors associated with invasion success

The final boosted regression tree (BRT) model for invasion success explained 41% of the variation in invasion success among species. The four most important variables in the invasion success model were global naturalization range size, minimum residence time, growth form and biogeographic origin (Figure 2a), which were also selected in the binomial GLM (Table S3.1, S3.4). No important

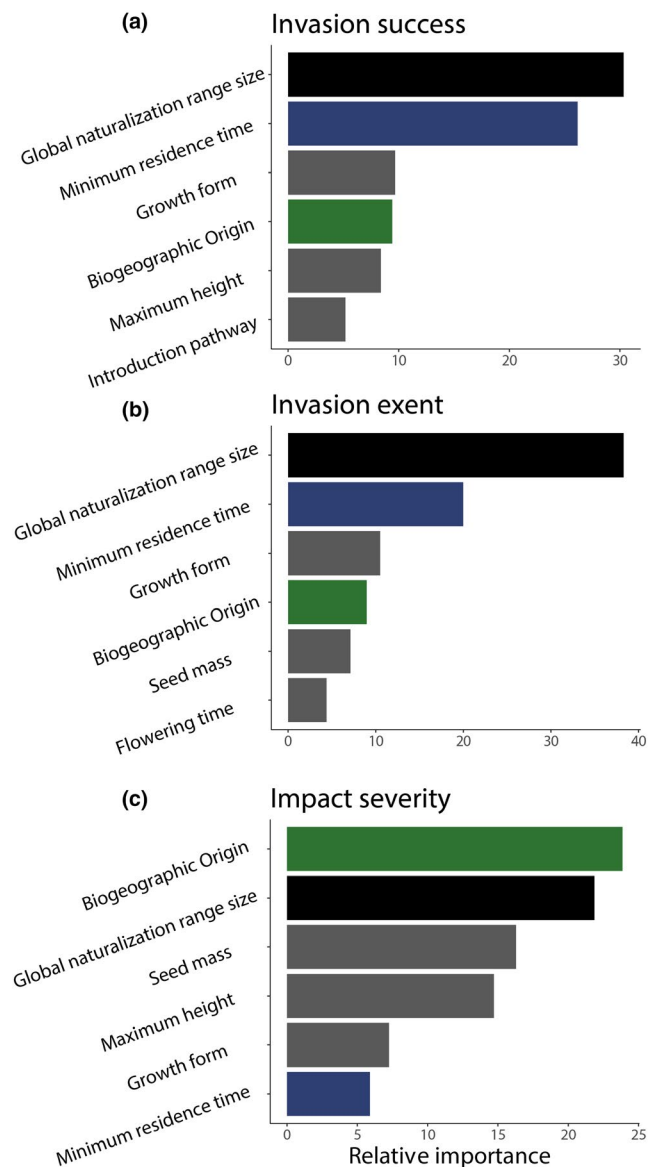


FIGURE 2 Relative importance of the six most important variables in the final BRT model for invasion success (a), the spatial extent of invasion (b) and the severity of invasion impacts (c). Variable relative importance was based on the number of times the variable was selected for splitting in the models, which is an indication of the proportion of variation it explained in the final BRT model. Bar colours indicate biological traits (grey), introduction history (blue), global naturalization range size (black) and biogeographic origin (green)

interactions were detected. The probability of successful invasion increased with increasing global naturalization range size and increasing residence time (Figure 3a,d; Table S3.4). Among the different growth forms, annual and biennial herbs were more likely to become invasive than non-native trees, shrubs, perennial herbs or liana species (Figure 4a), while plants originating in North America or Africa had a greater probability of becoming invasive than plants introduced from Oceania, Central and South America or Tropical Asia

(Figure 4d; Table S3.4). Maximum height was negatively associated with invasion success, but its effect was weak in the BRT (Figure 4g) and not detected at all in the GLM (Table S3.4). Unintentionally introduced plants with longer flowering times had a higher chance of becoming invasive plants, but these effects were minor, accounting for 5% or less of explained variation in the final BRT model (although GLM assigned relatively higher importance to introduction pathway; refer Supporting information Figure S1; Table S3.1).

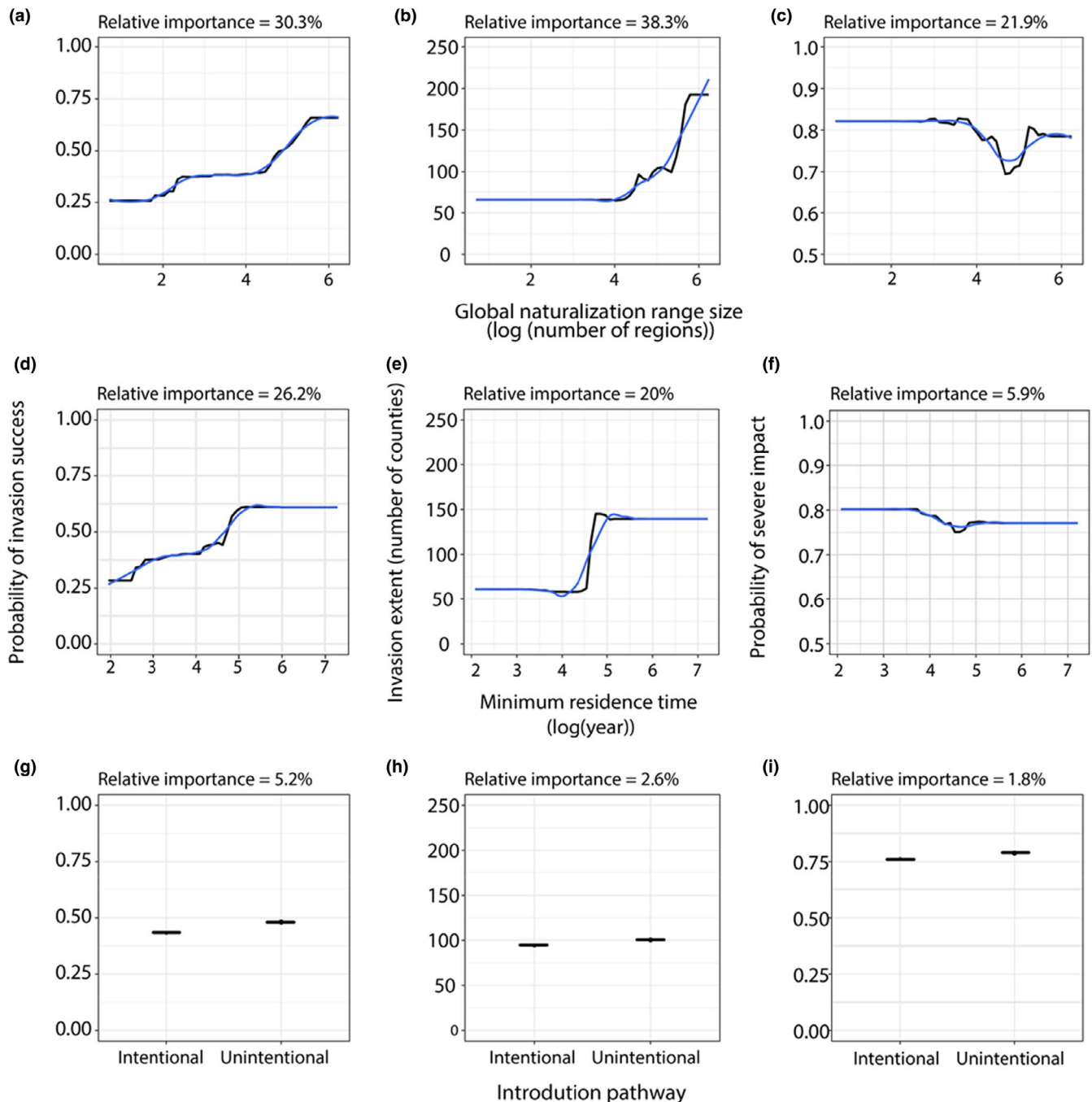


FIGURE 3 Partial response curves for invasion success (left column), invasion extent (centre column) and severity of impact (right column) as a function of species global naturalization range size (top row, panels a–c), minimum residence time (centre row, panels d–f) and introduction pathway (bottom row, panels g–i). In continuous explanatory variables, the black line shows the fitted function, and the blue line is a smoothed version showing the general trend. All continuous explanatory variables are log transformed. Refer also Figure 4

3.2 | Factors associated with the spatial extent of invasion

The final BRT model for invasion extent explained 47.8% of the variation in spatial extent among successfully invading species. The four most important variables in the invasion extent model were global naturalization range size, minimum residence time, biogeographic origin and growth form (Figure 2b), with all but biogeographic origin also identified in the GLM (Table S3.2, S3.5). No important interactions were detected. As with invasion success, invasive plants with larger global naturalization range sizes and longer residence time tended to have a greater extent of invasion (Figures 3b and 4e; Table S3.5; Figure S3.2). Among the different growth forms, annual and biennial herbs and lianas invaded a larger spatial extent than invasive trees, shrubs or perennial herbs (Figure 4b). Unintentionally introduced plants also tended to invade a larger area than intentionally introduced plants (Figure 3h; Table S3.5). In contrast with the results of invasion success model, plants originating in Oceania or Tropical Asia tend to invade a larger area than plants introduced from other regions (Figure 4e).

3.3 | Factors associated with the severity of invasion impact

Both BRT and GLM identified a different set of explanatory variables for severity to those identified for invasion success or extent of invasion. The BRT model explained 57.7% of the variation in impact severity among successfully invading species. The four most important variables were biogeographic origin, global naturalization range size, seed mass and maximum height (Figure 2c). GLM also identified four explanatory variables with biogeographic origin most important but identified mating system rather than global naturalization range (Table S3.3, S3.6). As was the case with invasion success, invasive plants introduced from the Americas (distributed across both North and South America) had higher chance of causing a severe impact (Figure 4f; Table S3.6). However, contrasting with invasion success, maximum height was a strongly positive predictor of the severity of invasion impacts (Figure 4i; Table S3.6), while minimum residence time was slightly negatively associated with impact severity (Figure 3f). Also contrasting with the results of invasion success, trees, shrubs, vines and lianas originating in Central and South America were associated with more severe impacts (Figure 4c,f). Introduction pathway had a similar role in impact severity as in invasion success, where unintentionally introduced species had a higher chance of causing a severe impact but again this effect was small (Figure 3i).

3.4 | Comparison of the factors influencing invasion success and impact

The relative importance of explanatory variables in the BRT invasion success model was strongly associated with that of the invasion extent

model (Pearson's $r = 0.933$, $p < .001$), but relatively weakly associated with impact severity model ($r = 0.426$, $p = .220$). The final invasion success model and invasion extent model shared the same four most important variables: global naturalization range size, minimum residence time, growth form and biogeographical origin (Figure 2a–b). While the corresponding GLM identified the same most important explanatory variables as BRT, it differed slightly in less important explanatory variables (Table S3.1–S3.6). Global naturalization range size and minimum residence time were both positively related to invasion success and invasion extent, and non-native plants with short life history (annual or biennial plants) tended to have both higher invasion success and invasion extent compared to other life forms. But among the four most important factors influencing invasion success, only biogeographical origin and global naturalization range sizes also played relatively important roles in the final impact severity model (Figure 2c), and their effects differed from those relating to invasion success (refer previous text). Meanwhile, seed mass and maximum height were both important and positively related to the severity of invasion impacts (Figure 4i,l), but relatively weakly associated with invasion success.

For invasive species, the fitted probability of invasion success had a significantly positive relationship with invasion extent (Figure 5a, $R^2 = 15\%$, slope = 3.92, $SE = 0.61$, $p < .001$). But invasive species having more severe-impacts did not differ significantly from those having only a mild-impact in their fitted probability of invasion success (Figure 5b, $t = 1.41$, $df = 152.49$, $p = .16$). These results suggest that similar factors influenced invasion success and the spatial extent of invasion, but different factors influenced the severity of invasion impacts.

4 | DISCUSSION

We provide, to our knowledge, the first study to consider the factors that determine both plant invasion success and invasion impacts over a near-continental extent. By analysing non-native plants in China, we found that their biological traits, introduction history and biogeographical origins were all strongly correlated with invasion success and impacts, but their relative importance in determining invasion success and invasion impacts differed. We found that unintentionally introduced non-native plants with shorter life cycles and longer residence times were more likely to become invasive and invade more a larger area, while taller plants introduced from the Americas tended to have more severe impacts on the invaded ecosystems. Moreover, both the BRT and GLM models agreed that the most important determinant of invasion success and extent of invasion (global naturalization range) differed from the most important determinant of severity of impact (biogeographical origin).

4.1 | Determinants of invasion success and extent differed from those affecting impact severity

Results support our first hypothesis, that invasion success and the spatial extent of invasion were influenced by similar factors

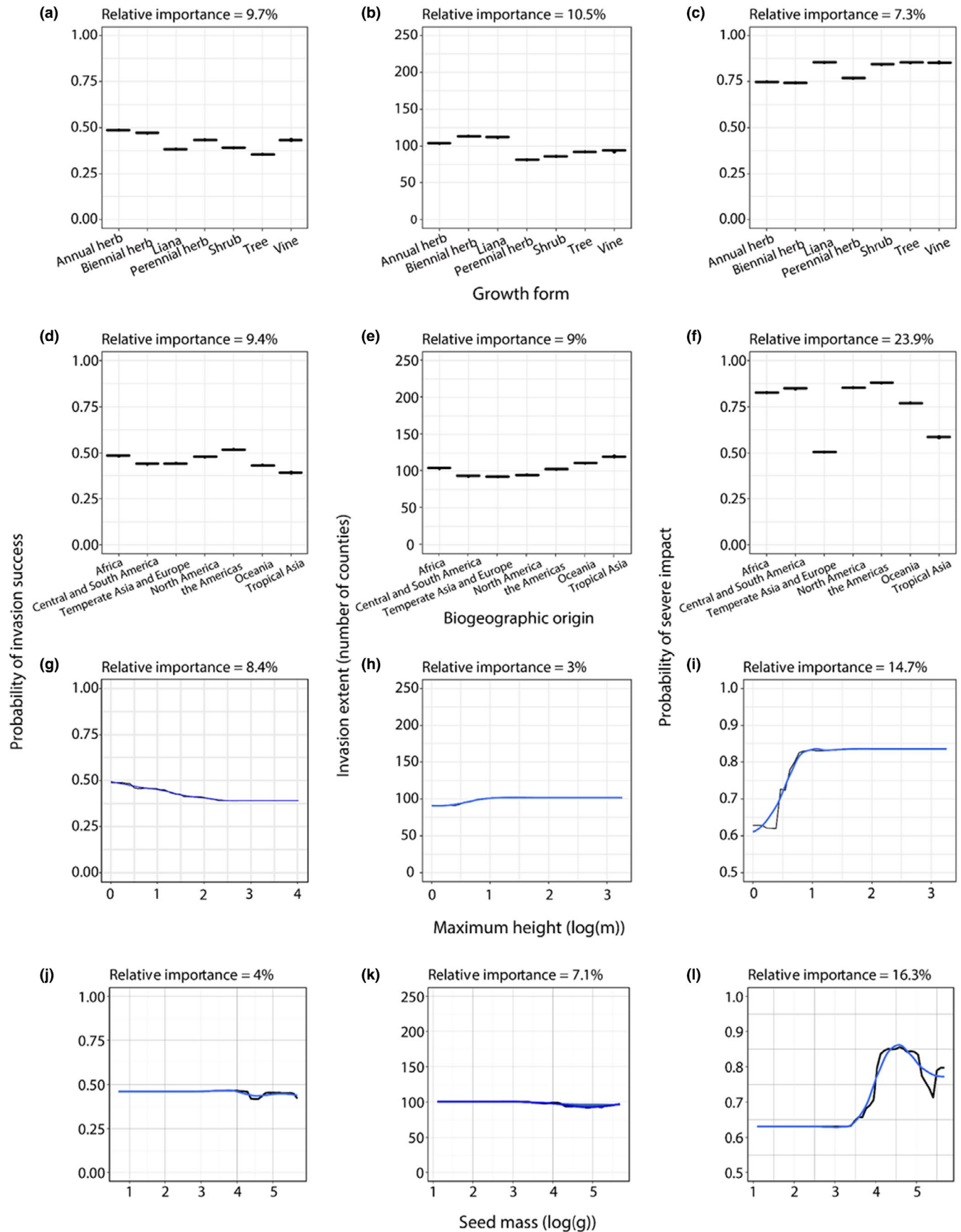


FIGURE 4 Partial response curves for invasion success (left column) and extent (centre column) and severity of impact (right column) as a function of species biological traits and origin: growth form (top row, panels a–c), biogeographic origin (second row, panels d–f), and maximum height (third row, panels g–i), seed mass (bottom row, panels j–l). In continuous explanatory variables, the black line shows the fitted function, and the blue line is a smoothed version showing the general trend. All continuous explanatory variables are log transformed. Figure S1.1 (Supporting Information) shows partial response curves for the remaining biological traits with relative importance <5%. Refer also Figure 3

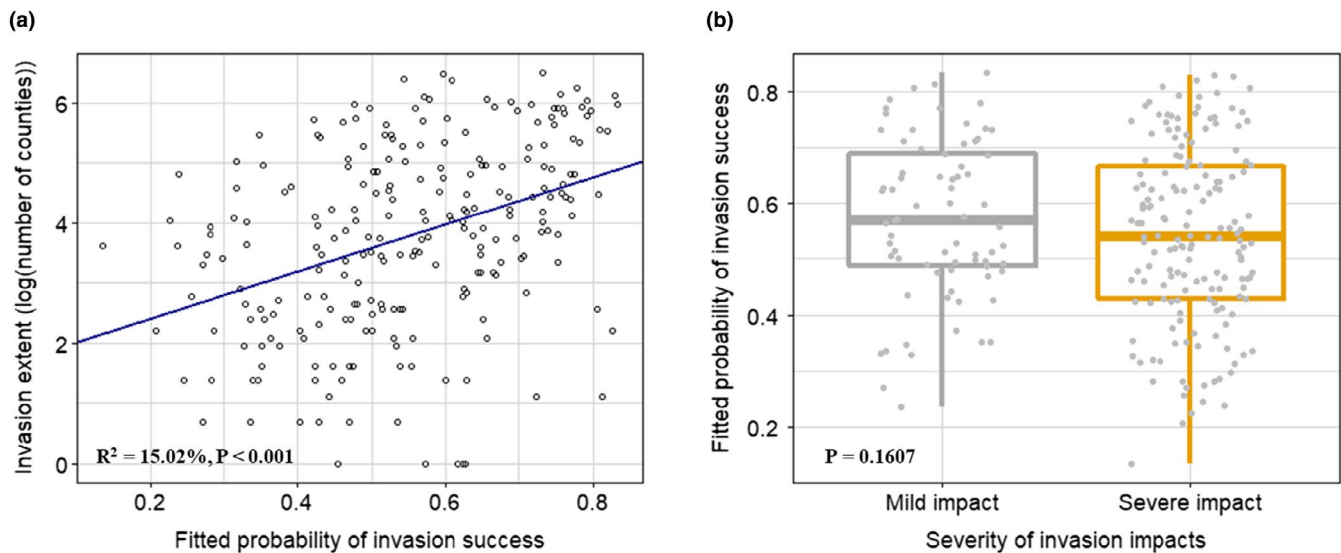


FIGURE 5 Comparison between the fitted probability of invasion success and real invasion impacts in invasive plant species. (a) The relationship between fitted probability of invasion success and the spatial extent of invasion. Blue line is fitted by general linear model. (b) The comparison of fitted probability of invasion success between mild-impact and severe impact invasive species. There is no significant difference between the two groups based on Student's *t*-test ($p > .05$)

associated with rate of spread and adaptive ability. Specifically, minimum residence time and growth form were the most important determinants of both invasion success and spatial extent of invasion. Newly introduced species usually confront disadvantageous conditions, such as the Allee effect, low genetic diversity and maladaptation to new environments, thus impeding their population expansion (Ni & Vellend, 2021; Pyšek et al., 2009). A short life history may facilitate population expansion and rapid evolution to adapt to new and heterogeneous habitats (Pyšek & Richardson, 2007), thus improving both the invasion success of naturalized plants and the spreading rates of invasive species. For long-life-history species, population expansion and adaptive evolution to new habitats could be much slower and harder, providing a possible explanation for the relatively few invasive tree species we observed.

Meanwhile, non-native species with longer residence times had a higher likelihood of becoming invasive, consistent with the effects of such characteristics on evolutionary adaptation (Simberloff, 2009). Although not directly associated with rates of spread, longer residence time can allow invasive species to spread to more locations, thus increasing invasion extent. In contrast, we found weak effects of residence time on the severity of invasion impacts in BRT (Figure 3f) and no effect according to GLM. Additionally, trees, shrubs and climbers (lianas and vines) tended to cause more severe impacts than other life forms, consistent with a growing body of evidence that many trees and shrubs have an increased probability of becoming noxious

invasive plants as they successfully spread to new habitats (reviewed in Richardson & Rejmánek, 2011). This implies that some features beyond evolutionary adaptation and population expansion determine the severity of invasion impacts (Pyšek et al., 2012).

The positive relationship between plant maximum height and impact severity for invasive plants was consistent with our second hypothesis, and possibly due to the competitive advantage it provides (Figure 4i, Vilà & Weiner, 2004). For example, shoot height is likely to be associated with a plant's ability to intercept light and to inhibit the growth of neighbouring individuals (Keddy et al., 1998), and therefore it is critical in shaping plant competitive hierarchies. Both theoretical and empirical studies have proposed that competition could have deterministic effects on impact severity (Levine et al., 2003; Pyšek et al., 2012). Logically, other functional traits related to plant competitive ability that were not included in this study, such as root architecture (Ni et al., 2018), photosynthetic rate and resource use efficiency, could also be correlated with impact severity. The lack of functional trait information impeded such tests in this study and the on-going development of functional trait databases (e.g., TRY, <https://www.try-db.org/TryWeb/Home.php>) will help researchers to incorporate these traits in future work.

Seed mass was positively related to the severity of invasion impacts (Supporting information, Figure 4l). It is possible that plants with large seeds tend to have larger seedlings (Moles, 2018), providing an advantage in the intense competition of the establishment

phase (Ni et al., 2018). In contrast, seed mass was weakly associated with invasion success or extent. Some have hypothesized that small seeds could disperse farther, thus improving invasion success and the spatial extent of invasion (e.g., Pyšek et al., 2012). But recent studies have revealed positive relationships between seed mass and seed dispersal distance, while plant height, growth form, dispersal syndrome and terminal velocity were better explanatory variables of species' dispersal ability than was seed mass (reviewed in Moles, 2018).

Global naturalization range size (the number of regions that non-native species have colonized outside native regions) had positive effects on both invasion success and invasion extent, but slightly negative effects on impact severity. It is possible that both invasion success and extent would be increased by the same intrinsic features that facilitate plant naturalizations worldwide, or that their larger range size simply increases propagule pressure with the same result. However, traits that affect global naturalization range size seem unlikely to influence interactions with native species, potentially explaining the weak association with impact severity. Despite only having a small effect size, an unintentional introduction pathway increased both invasion success and impact. This result is inconsistent with some previous studies, which found intentionally introduced plants were more likely to become invasive (Thuiller et al., 2006). A possible reason for this is that China has experienced less plant introductions before 1800 AD than some other studied regions (mostly Europe and North America). Any unintentionally introduced species might have successfully invaded other regions earlier, allowing time to establish the large population sizes that would facilitate their introduction to China via multiple pathways associated with trade or human movement.

In both of our results, longer flowering time tended to increase invasion success (Figure S1.1c; Table S3.4), while monoecious invasive species tended to cause more severe invasion impact than species with other mating systems (Figure S1.1i; Table S3.6), albeit with limited effect size (accounting for <5% of explained variation). It is possible that these two traits have scale-dependent effects, exerting a relatively weak influence over larger spatial scales. This would then increase the probability of finding effects of flowering phenology on invasion impacts over smaller spatial extents (e.g., Alexander & Levine, 2019).

Our findings also improve our understanding of non-native species' geographical distributions outside native regions, which is an important question in biogeography (Gaston, 2003; Ricklefs et al., 2008; Wilson et al., 2007). For example, Ricklefs et al. (2008) found that herbaceous non-native plant species tended to have larger range sizes outside native regions than woody (tree and shrub) species in either Eastern North America or East Asia. In this study, we found that not only growth form but introduction history and biogeographical origins can also strongly influence species' geographical distributions outside native regions. To our knowledge, this is the first study to find a positive relationship between invasion extent and global naturalization range size. While the underlying mechanisms (propagule pressure and/or intrinsic traits) remain unclear, this warrants further study.

4.2 | The role of biogeographical origins

Identifying species functional differences between biogeographical regions is a core question in biogeographical studies (Cox et al., 2016) and we found clear evidence that species from different biogeographical origins differ in their invasion success and impact. The effects of biogeographic origin on invasion success or impacts are usually indirect, that is, they occur by influencing species' evolutionary history, environmental adaptation and propagule pressure (Peoples & Goforth, 2017). The smaller likelihood of those naturalized plants introduced from Oceania, Tropical Asia and Central and South America shifting to invasive plants might be due to climatic mismatches between these regions and their invaded ranges in China. These three biogeographical regions have a mainly tropical (rainforest/savanna) climate, but most invasive species were distributed in eastern China (Ma, 2014), where is mainly of temperate or subtropical climate. Species from these regions may need more time to adapt to the new climatic conditions, delaying or preventing them from spreading widely from points of origin.

Also contrasting with the results of the invasion success models, non-native plants introduced from Central and South America tended to be associated with more severe impacts once becoming successfully invasive. Some have pointed out that invasive species from Central and South America are usually highly competitive, combining fast growth rates and high resource acquisition ability (Ma, 2014). According to the evolutionary imbalance hypothesis proposed by Fridley and Sax (2014), this might be because plants from Central and South America faced a greater array of competitors historically and thus have evolved a higher competitiveness than invasive plants from less competitive environments. There could be several reasons that non-native plants originating from North America could have higher impact severity in China. First, long-distance isolation might mean non-native plants from the Americas escape specialized enemies resulting in improved performance (Heckman et al., 2016). Second, the high environmental similarity between East China and Eastern North America suggests that species from these regions will share similar niche dimensions. Any resulting strong niche overlap with native species would increase the competition intensities between invasive and native species according to contemporary coexistence theory and result in greater impact severity (MacDougall et al., 2009). However, empirical knowledge of the mechanisms behind origin effects such as these is scarce, and more effort is needed to elaborate on these processes.

4.3 | The multiple dimensions of invasiveness

Invasiveness is a synthetic concept that can be defined from multiple invasion stages (van Kleunen et al., 2010). These include but are not limited to the three measures used in this study, with other measures including introduction success or naturalization success. Each of these different dimensions of invasiveness could be associated

with different determinants. For example, Milbau and Stout (2008) found that species naturalization and invasion had different associated factors (e.g., clonal growth could significantly influence plant naturalization success but had no effect on invasion success). Our results suggest that different factors are associated with successful invasion and spread from those resulting in severe impacts, and these disparities suggest that the relative importance of factors associated with invasiveness could change across the invasion process as the underlying mechanisms (e.g., competition, environmental adaptation and dispersal) differ (Carboni et al., 2016). Thus, reconstructing the stage-dependent processes in invasion dynamics (e.g., introduction success, naturalization success, invasion success and invasion impacts) is a promising direction for more accurate assessment of invasion risks and could inform more effective invasion management (Pyšek & Richardson, 2007).

Although we consider only a binary definition of impact severity, multiple forms of environmental impact can be described (refer Blackburn et al., 2014; Nentwig et al., 2016) and these are also context dependent (Kumschick et al., 2015). For example, the mechanisms causing decline in native species populations and changes in the nitrogen cycle in native ecosystems can be different; and the magnitude and invasion impacts could change across habitats as local species composition and/or abiotic environments change. Figuring out how different factors influences non-native species' impact severity at different impact dimensions and environmental context deserve future studies.

4.4 | Implications for plant invasion controls

We foresee two potential applications for our findings. First, due to the diverse range of habitats and types of non-native plant species in China, our results provide general inference on the role of the different plant characteristics on invasion success versus invasion impacts compared with studies done over a smaller geographical or taxonomic range (Cadotte et al., 2006). Second, from a risk management perspective, invasion success and invasion impacts could be viewed within a risk assessment context, as the likelihood and consequences of a species becoming invasive. Findings thus provide new insights to understand and respond to invasion and potentially to the prioritization of species for interventions. Although many non-native species introduced during recent years have not caused impacts to native ecosystems (van Kleunen et al., 2019), some of these could possibly become severe invaders once they successfully spread, especially highly competitive species. More attention should be paid to the risks associated with tall plant species originating in the Americas as these were associated with the most severe impacts.

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AUTHOR CONTRIBUTION

MN designed the study and collected the data. MN analysed the data with help from DD. MN, DD, SL, YW, XS, HX, CC, FH and SF wrote the manuscript. All authors approved the final manuscript.

DATA AVAILABILITY STATEMENT

All data will be available upon publication.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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