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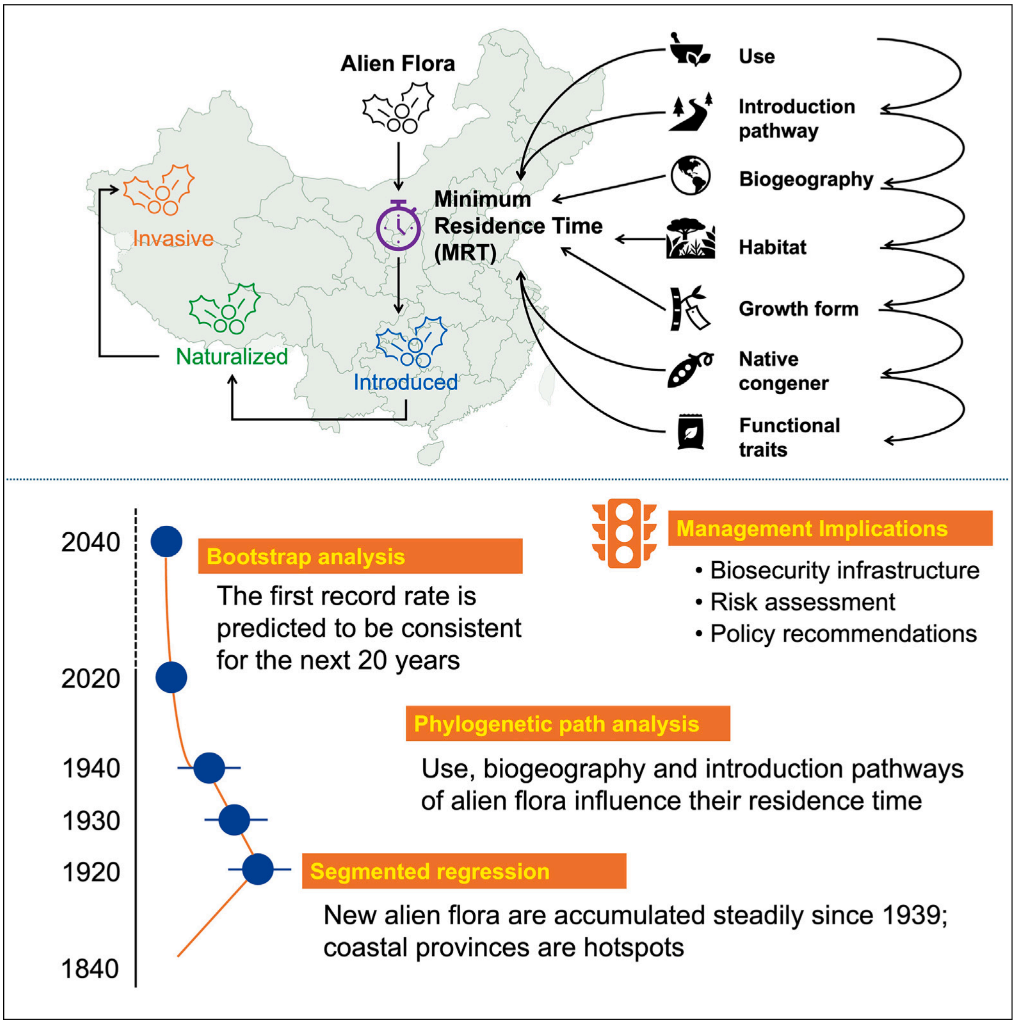

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Highlights

Spatiotemporal pattern of alien flora accumulation was studied at a national scale

New alien flora is accumulating at a constant rate in China

Different factors influence their residence time depending on their invasion status

The trend will remain consistent in the foreseeable future

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Alien flora are accumulating steadily in China over the last 80 years

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SUMMARY

New alien species are increasingly introduced and established outside their native range. The knowledge of the spatiotemporal dynamics of their accumulation and the factors determining their residence time in the introduced range is critical for proactive management, especially in emerging economies. Based on a comprehensive time series dataset of 721 alien angiosperms in China, we show that new alien flora has been accumulating steadily in China, particularly in the coastal regions, for the last 80 years without saturation. The ability to occupy a large number of habitats facilitates the early introduction of alien flora, whereas a large naturalized range, greater number of uses, and multiple introduction pathways directly contribute to their naturalization and invasion. The temporal pattern is predicted to remain consistent in the foreseeable future. We propose upgrading the country's biosecurity infrastructure based on a standardized risk assessment framework to safeguard the country from ongoing and future invasions.

INTRODUCTION

Biological invasions are widely recognized as one of the most severe threats to conserving natural resources, biodiversity, and sustainable livelihoods.[1] Rapid globalization and climate change are facilitating and intensifying the spread of invasive alien species.[2,3] Previous studies have shown that the introduction of new alien species is increasing, the pattern of which varies between taxonomic groups and geographic regions.[4,5] While these variations are observed at global and continental scales, we know little about the spatiotemporal dynamics of new alien species accumulation at a national scale.

Furthermore, after introduction to novel geographic regions,[6] a subset of the introduced species becomes naturalized (maintains self-sustaining populations for multiple generations) and invasive (overcomes the dispersal barrier to spread into novel environmental conditions).[7] Several factors act interactively to move the alien species along this time-dependent invasion process (introduction-naturalization-invasion continuum). One such factor is the residence time, usually approximated by minimum residence time (MRT), which varies across stages of the invasion process.[8]

The MRT of a species is defined as the time since the alien species was first recorded in the introduced range.[9] Longer presence may increase the likelihood of an alien species overcoming its lag phase,[10] increase the propagule pressure,[11] and enhance the eco-evolutionary mechanisms that potentially help the alien species occupy a large adventive range.[12] The MRT has often been considered a covariate of successful naturalization and invasion.[13–15] However, the biotic and abiotic factors, which can influence successful naturalization and invasion of alien species, can also influence the residence time of alien species. For example, plant functional traits were found to indirectly influence the successful naturalization of alien plant species (e.g., in Europe[16] and Germany[17]) by mediating the residence time of the species. Similarly, abiotic factors, like uses,[18] introduction pathways,[19] and biogeographic range size,[20] can also influence the residence time of alien species. However, very few studies have investigated the influence of biotic and abiotic factors on the MRT of the alien species.[9] It is also possible that considering the MRT as a covariate for successful naturalization and invasion could have masked or misinterpreted the effects of the biotic and abiotic factors on the MRT.[21]

The knowledge gaps of the temporal dynamics of new alien species accumulation at a national scale and the relative influence of different variables on their residence time are more prominent for emerging economies. Accelerated globalization of trade and climate change are facilitating novel invasions in these countries,[22,23] which often lack the required response capacity to deal with this threat.[24] Compared to the first wave of globalization (1850–1914, among European countries and their former colonies[25]), the second wave (1960–today) is facilitating the spread of more invasive species by creating diverse trade routes, providing equal trade opportunities among countries, and generating new economic powers.[26] The spread of invasive species is also facilitated by climate change, as a high tolerance for fluctuations in environmental conditions is helping the invasive species to adapt to the effects of climate change.[27] Moreover, compared to the developed

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economies, the potential impacts of climate change on the developing world are more severe due to limited response capacity and heavy economic dependence on climate-sensitive sources.[28]

Addressing these knowledge gaps is, therefore, crucial for developing country-level policy interventions and facilitating research and development.[29] China can be an ideal representative of emerging economies to address these knowledge gaps because of its long history of alien plant introduction,[30] the diversity of alien species' life forms,[31] and its vulnerability to novel invasions due to the gradual opening of its economy to the global markets since the 21st century. Very few studies have been conducted so far to map the spatiotemporal pattern of alien flora distribution in China. However, such pattern was deciphered either for the invasive aliens only[32] or for a subset of alien flora present in China.[33] Similarly, studies have been conducted to decipher the relationship between residence time and invasion success of alien plant species in China[34–37], yet the interactive influence of biotic and abiotic factors on their residence time is yet to be investigated.

Our objectives of this study are 2-fold: 1) to identify the spatiotemporal pattern of new alien plant species accumulation and 2) to decipher the relative influence of the biotic and abiotic variables on their residence time in China. To address these objectives, we used 180 years of time series data of the first occurrence record of 721 alien plant species. We fitted five functions and used two regression models to analyze the temporal change of the first record rate. Following the global pattern,[5] we expected an increasing trend of new alien species accumulation in the country over time. To analyze the spatial pattern of new alien flora accumulation, we mapped the distribution of their first records at the provincial level. Following the previous studies on the spatial pattern of alien flora distribution in China,[33] we expected that the first recorded locations will be concentrated in the coastal regions. We further collected data on ten biotic and abiotic variables related to functional traits, uses, biogeography, and introduction pathways. Phylogenetically adjusted regression models were used to identify the variables' influence on the MRT, with a hypothesis that both biotic and abiotic variables would influence the residence time of the alien plant species in China. We finally discussed how the temporal trend of plant invasion and the influence of biotic and abiotic variables on the MRT of the alien species could be used to strengthen the existing biosecurity infrastructure of the country against future large-scale plant invasion events.

RESULTS

Spatiotemporal trend

The analysis of the time series data revealed that the five fitted functions were equivalent in modeling the temporal change of the first record rate of the Chinese alien flora, as the differences between the pairwise Akaike information criterion (AIC) values were less than five (Table S1). After removing the two outliers from the data, the saturating function with the lowest AIC could significantly explain the temporal trend of the first record rate (estimate $\pm$SE = 4.39 $\pm$ 0.41, 95% confidence interval [CI] = 3.71–5.12). The pattern was consistent for the naturalized and introduced species (Figure S2). For the invasive aliens, the linear function had the lowest AIC value, although the negative temporal trend of the first record rate over time was not significant.

The segmented regression analysis found the breakpoint in the year 1918 (standard error $\pm$ 8.27) with significant slope parameters (estimate $\pm$SE = 0.089 $\pm$ 0.02, $p < 0.001$) (Figure 1A; Table S2). The breakpoints varied between alien species of three invasion categories, with the earliest and latest breakpoints observed for the introduced (1910 $\pm$ 11.72) and invasive (1921 $\pm$ 9.3), respectively (Figures 1B–1D). The linear regression models fitted with the post-breakpoint data revealed a significant decrease in the first record rate since 1918 (estimate $\pm$SE = -0.062 ± 0.01, $p < 0.001$). The first record rate decreased significantly till 1926 and stabilized in 1934 (Figure 1A; Table S3). The earliest stability of the first record rate was achieved by the introduced aliens (in 1922), followed by the naturalized (in 1938) and invasive (in 1939) aliens (Figures 1B–1D).

The bootstrap analysis showed that the first record rate of the alien species would remain consistent for the next 20 years (Figure 2). The average (of 1,000 simulated datasets) first record rate of alien species in 2030 was found to be 2.63 (95% CI: 1.42–3.77), and in 2040 the value was 2.57 (95% CI: 1.18–3.95) (Figure 2A). Among the three invasion categories (Figures 2B–2D), the predicted first record rate was maximum for the naturalized aliens and minimum for the invasive aliens.

The first-recorded sites of the alien plant species in China were mainly distributed in the coastal region (Figure 3). Throughout the 180 years (1840–2020), the Guangdong province of south China (zonation of the provinces following[32]) has remained the hotspot of first-recorded sites of the alien species of all three invasion categories. Since 1920, southwest China's Yunnan province became an additional hotspot of the first-recorded locations. The other provinces with 5%–10% of the first records were mainly distributed in the coastal regions (e.g., Fujian and Shandong in east China) (Figure 3). Over time, the first detection sites of the invasive and naturalized aliens decreased. In the last 50 years, the invasive aliens were first detected mainly from the coastal provinces of east China, whereas the naturalized aliens were detected from the southwest provinces. The first detection sites of the introduced aliens moved toward the north and northwest provinces over time, although the hotspot remained in the south and southwest provinces (Figure 3).

Comparison of MRT across invasion status and variable categories

Among the three invasion categories, the invasive aliens had the highest MRT value (mean $\pm$ SE = 98.55 $\pm$ 2.47), followed by the naturalized (92.64 $\pm$ 2.68) and introduced (85.83 $\pm$ 3.38) aliens. The MRT values differed significantly across the three categories of alien species (χ^2 = 6.133, degrees of freedom [df] = 2, $p = 0.047$), and the *post hoc* comparisons between the categories revealed a significant difference ($p = 0.043$) between the MRT values of the invasive and introduced aliens.

For the invasive alien species, the average MRT values were lowest (latest introduction) for the herbaceous growth form, having non-vertebrate poison use, belonging to the brackish habitat, introduced as escapees from confinement, originated in Australasia, and naturalized in Northern America (Figure 4; Table S4). The average MRT values were lowest for the naturalized alien species with herbaceous growth form,

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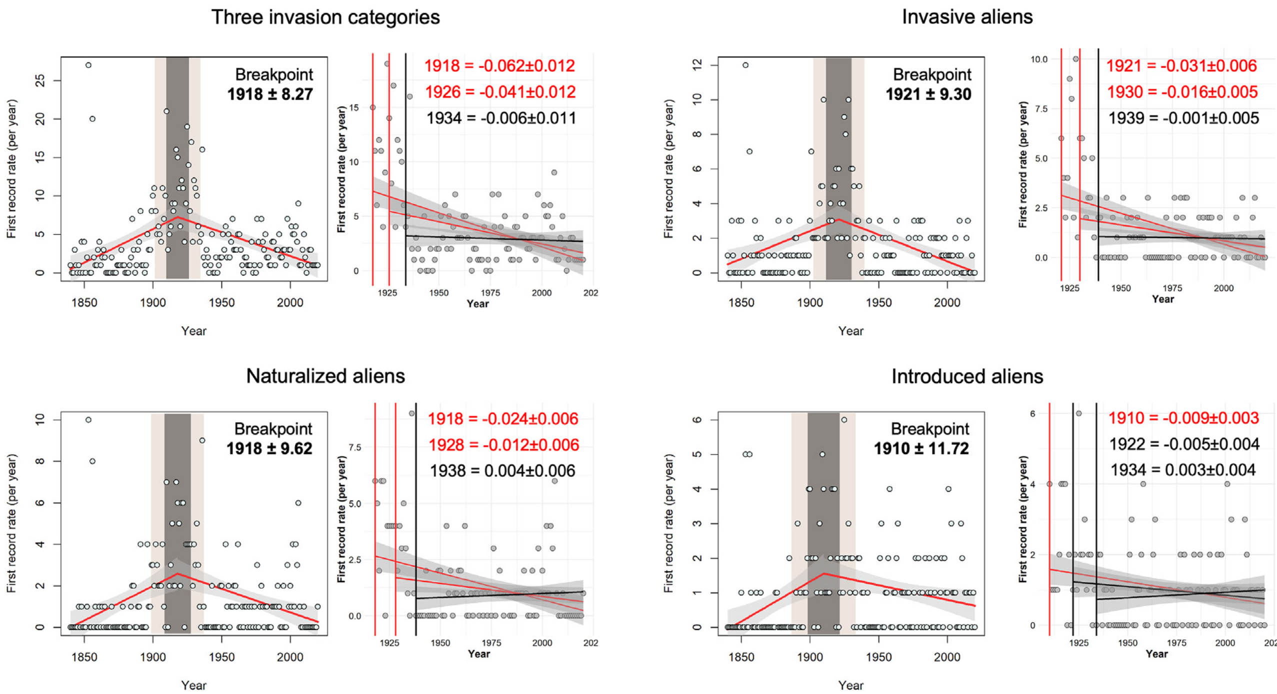

Figure 1. Temporal trend of accumulation of the Chinese alien flora

Results of the segmented regression analyses to identify the breakpoints (left panel) and the linear regression models to identify the temporal trend of the first record rate (right panel) for the three invasion categories together and separately. The coefficients and standard errors of the linear regression models are provided. Significant (at $p < 0.05$) slopes of the regression models are marked in red.

being used as gene sources, belonging to the freshwater habitat, introduced as escapees from confinement, originated in Southern America, and naturalized in Australasia. For the introduced alien species, the average MRT values were lowest for the species with tree growth form, having fuel uses, belonging to the brackish habitat, introduced as transport contaminant, originated in Southern America, and naturalized in Australasia. The two-way ANOVA revealed significant differences between 1) the variable categories for two variables (habitat and native range), 2) the invasion categories for two variables (introduction pathway and naturalized range), and 3) both variable categories and invasion categories for one variable (use) (Figure 4; Table S4).

Influence of biotic and abiotic variables on MRT

The phylogenetic tree revealed that the 721 species belonging to 402 genera within the three invasion categories were widely distributed among major angiosperm clades (Figure S3). Six of the ten variables considered in this study showed significant (at $p < 0.05$) phylogenetic signals for both Blomberg's K and Pagel's λ, although the pattern varied across invasion categories (Table S5). The phylogenetic generalized least squares (PGLSs) analysis revealed significant positive effects of specific leaf area (SLA), number of uses, introduction pathway, habitat, and naturalized range size on the MRT of Chinese alien flora (Figure 5; Table S6). Significant positive effects of the number of uses and naturalized range size on the MRT were observed across the three invasion categories. Besides, SLA and number of introduction pathways (invasive and naturalized aliens), native range size (invasive and introduced aliens), and number of habitats (naturalized and introduced aliens) also significantly influenced the MRT depending on the invasion status of the alien species (Figure 5; Table S6).

The phylogenetic path analysis (PPA) with partially imputed data identified 155 phylogenetic regressions, of which 51 were unique. After setting the regression coefficients for the absent paths to zero, the path averaging revealed strong (coefficient >0.2) and direct positive effects of naturalized range size and number of uses on MRT of all alien species (three invasion categories together) as well as for the invasive and naturalized aliens. For the introduced aliens, MRT was influenced by naturalized range size and number of habitats (Figure 6; Table S7). Other variables indirectly affected MRT by influencing the naturalized range size (all aliens, invasive, and naturalized aliens) and number of uses (introduced aliens). Specifically, the naturalized range size was positively influenced by the number of uses (all aliens, invasive and naturalized aliens) and native range size (naturalized aliens) and negatively influenced by growth form (all aliens, invasive and naturalized aliens) and height (invasive aliens). The number of uses was positively influenced by growth form and naturalized range size for the introduced aliens.

The PPA with the non-imputed data of a subset of species revealed a direct positive effect of naturalized range size on the MRT of alien species across the three invasion categories (Table S8), thus being consistent with the findings of the partially imputed data. However, the indirect effects of variables on MRT were mediated by the native range size (all aliens, invasive and naturalized aliens) and number of habitats (introduced aliens).

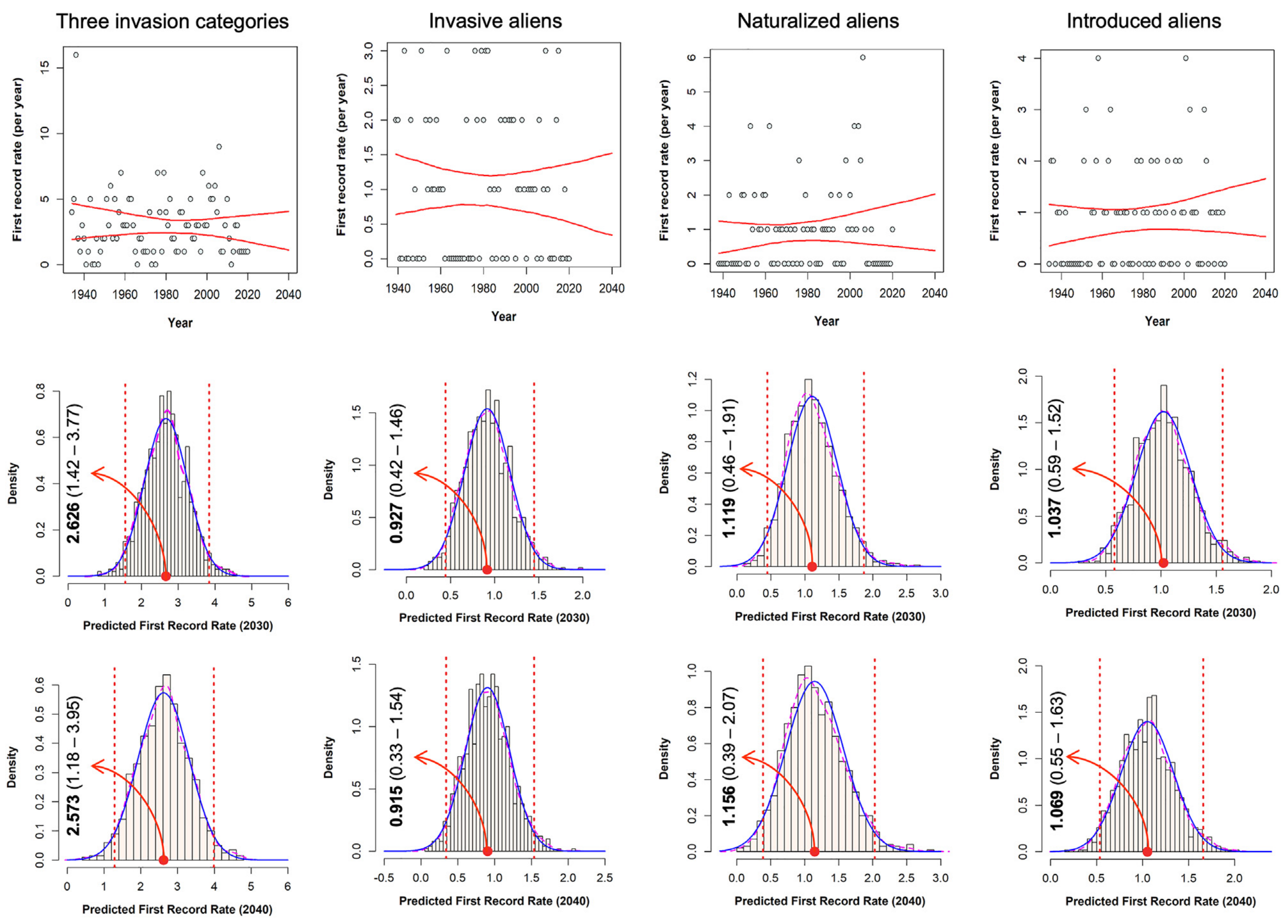

Figure 2. Prediction of the temporal trend of Chinese alien flora accumulation

Results of the bootstrap analysis to predict the temporal trend of the first record rate in two future time points (2030 and 2040) for the three invasion categories together and separately. The top panel of each subplot shows a 95% confidence interval of the bootstrap estimates. The histograms in the middle (for 2030) and bottom (for 2040) panels are approximated by kernel density (marked in magenta dotted line) and normal density (marked in blue solid line) functions. 95% confidence intervals are shown using red colored dotted vertical lines, and the average number of predicted first records is presented using a red colored dot.

The least absolute shrinkage and selection operator (LASSO) regression analysis revealed that Africa, Asia-Temperate, and Northern America as the naturalized ranges influenced the MRT of the alien species (Table S9). Among the 13 use categories, food, animal foods, materials, medicines, and environmental uses significantly influenced the MRT. The MRT of the invasive aliens was influenced only by four categories of uses (food, materials, invertebrate poison, and medicines); that of the naturalized aliens was influenced by uses (food and medicines) and naturalized range (Africa and Northern America), and that of the introduced aliens was influenced only by a single category of habitat (terrestrial managed).

DISCUSSION

No saturation of alien flora

Our study shows for the first time at a national scale that the first record rate of alien plant species does not show any increasing trend in China for the last 100 years, thereby refuting our first hypothesis. The pattern is consistent for alien species of three invasion categories. In the last 180 years of temporal data considered in this study (1840–2020), the only significant increase of the first record rate was observed during the 1910–1930 time period. This time frame in the history of China has often been characterized as the time when scientific progress peaked after the formation of the Republic of China in 1912. [38] Although there was a significant drop in the first record of alien species in China after this time period, possibly due to the political unrest in the country, we observed stability in the first record rate since 1940. This finding indicates that new alien species are being reported at a constant rate to date, with sporadic increases in new reports (e.g., in 2010), and there is no sign of saturation of alien plant species in China. Of course, the government's increased biosecurity vigilance over time has kept the number of new alien species in check. However, these regulations may not be effective enough to prevent the introduction of new alien species into China, [11] as we observed no significant decrease in the first-record rate over the last 80 years.

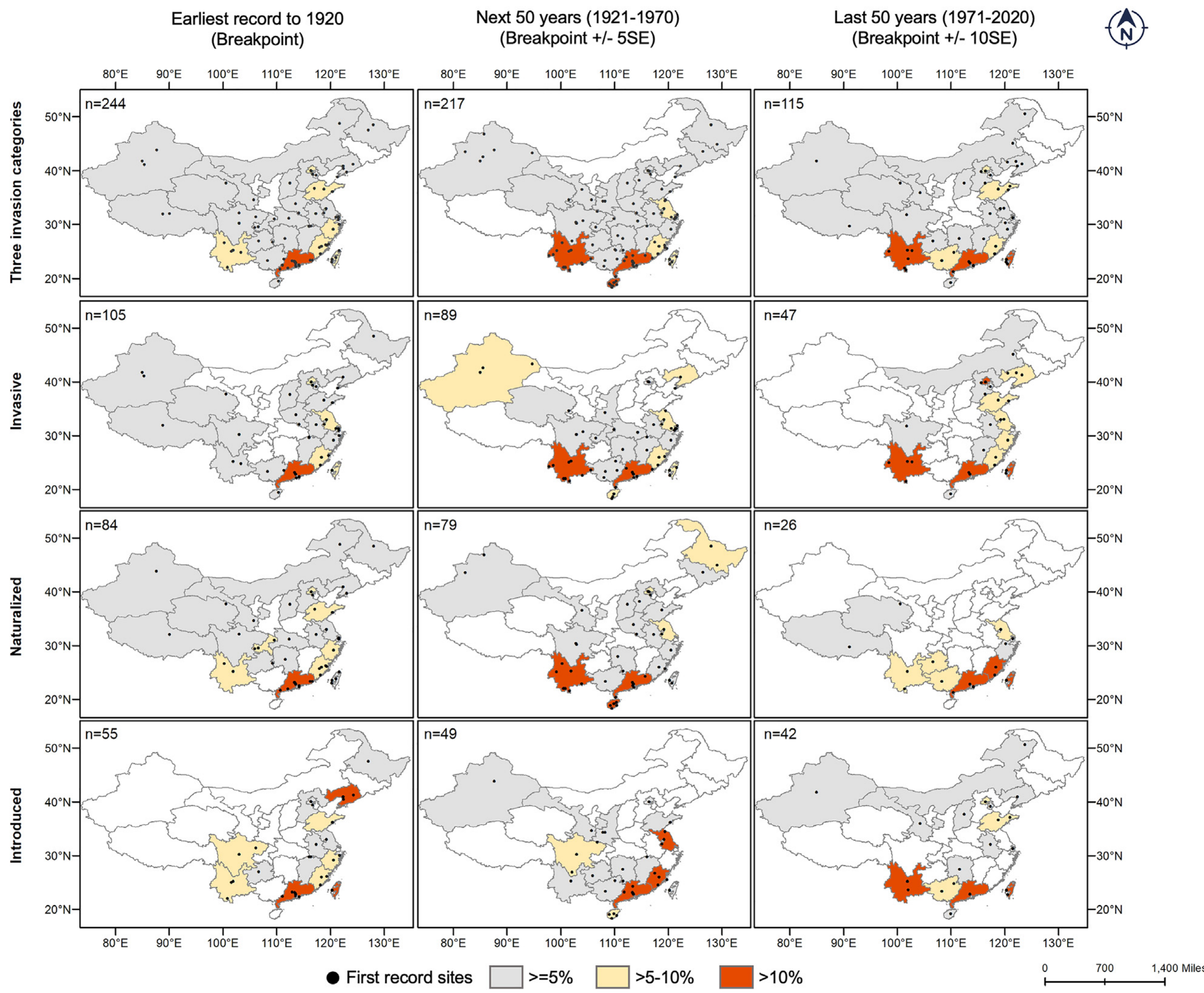

Figure 3. Spatial pattern of alien flora accumulation in China

The distribution of the first recorded locations of the three categories of alien plant species in China across three time periods. The provinces were color-coded based on the percentage of the first recorded locations. The 180-year time considered in this study (1840-2020) period was divided into three periods: earliest record date to 1920 (first 80 years covering the breakpoints of all alien species), 1921–1970 (next 50 years covering the breakpoints ± 5 standard errors of all alien species), and 1971–2020 (last 50 years covering the breakpoints ± 10 standard errors of all alien species). The number in each map corresponds to the total number of first recorded locations in each period.

The temporal trend of the first record of the Chinese alien flora, therefore, agrees with the global [5] and Chinese [33] non-saturating pattern of new alien species accumulation but contradicts the increasing trend (exponential, in the case of China) of the same and the decreasing trend in the number of alien species in the European Union. [39] Data resolution is one possible reason for the contradictory findings between these studies. Focusing on the national level, we collected data at a higher resolution for a larger number of vascular plant species (721 species compared to the 299 plant species of the Global Alien Species First Record Database,[5] and 265 plant species in China[33]). The first record data of the alien plant species used in this study were collated from bibliographic repositories and digitized herbarium databases, which increased the resolution of the data manyfold compared to the previous study. Our study, therefore, supported the importance of herbarium data in invasive species research, e.g., to study the pattern of range expansion of alien species [40] and assemble national-level checklists of alien species,[41] especially for the countries where global databases are often incomplete.

However, in accordance with the previous study,[33] we found that the first recorded locations of the alien flora were concentrated in the coastal regions of south, southwest, and east China. This pattern can be explained based on socioeconomic and environmental factors. Firstly, the provinces of south, southwest, and east China are historically engaged with international trade. Notable is the Guangdong province of south China, which has remained a key point of international business via its capital of Guangzhou city since the 19th century.[42] Therefore, unsurprisingly Guangdong province has remained a hotspot of the first recorded locations of the Chinese alien flora for the last 180 years. Moreover, these provinces have higher urbanization rates, per capita gross domestic product (GDP), and population densities than

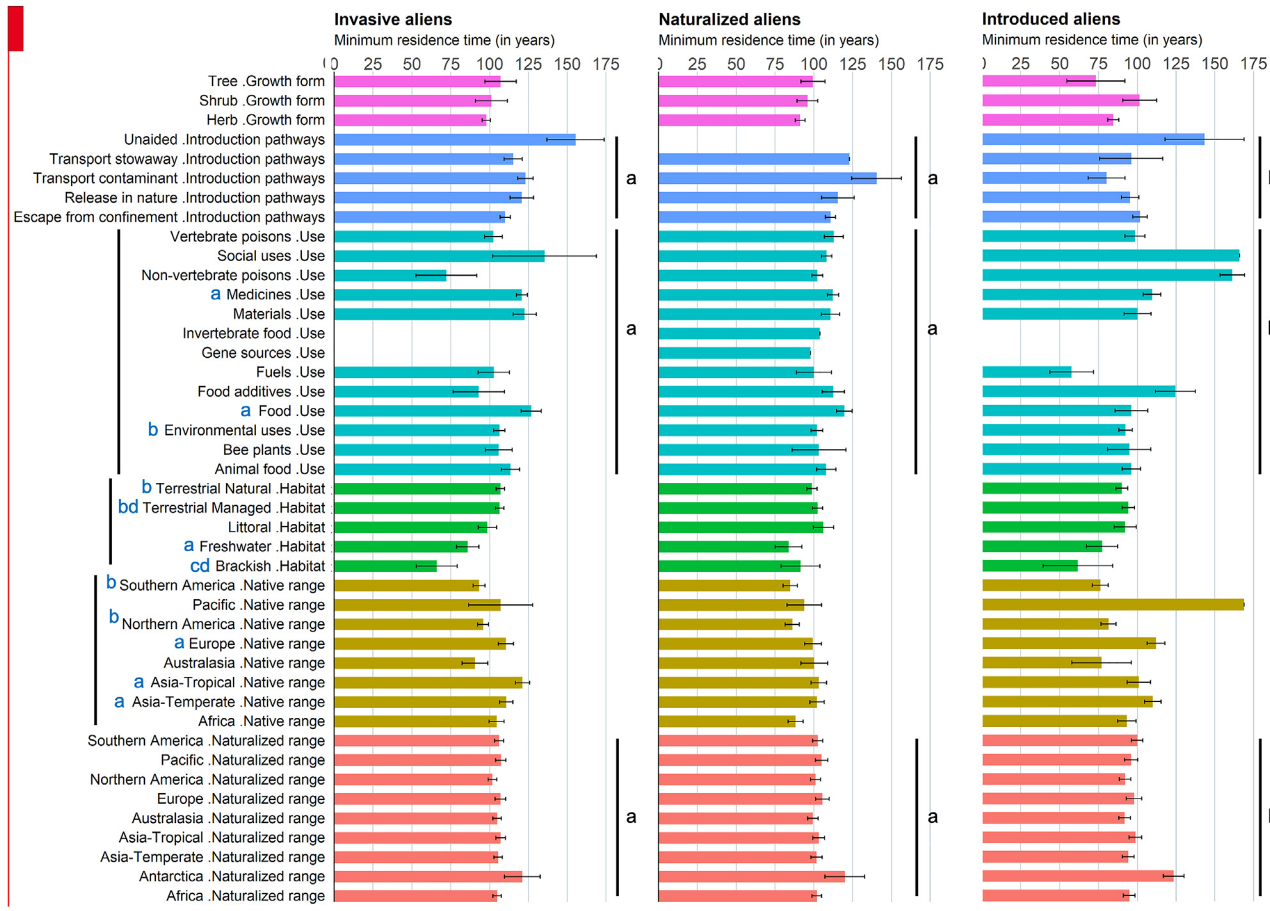

Figure 4. Results of the two-way ANOVA showing differences in the MRT (minimum residence time) values between the variable (biotic and abiotic) categories for three categories of alien flora

The variable categories are at TDWG (International Working Group on Taxonomic Databases for Plant Sciences) level 1. The bars represent the mean (± standard error) MRT value for each variable category. Different variables are marked in different colors. Different letters along the variables' names (left) indicate significant differences (at $p<0.05$ level) between the categories irrespective of the invasion categories. Different letters along the bars (right) indicate significant differences (at $p < 0.05$ level) between the invasion categories for a variable.

the inland provinces.[43] While the international trade routes might have facilitated new alien species introduction into these regions, anthropogenic activities and socioeconomic infrastructure might contribute to the establishment and spread of the alien species by increasing propagule pressure.[44] Secondly, these provinces are characterized by tropical or subtropical climates, similar to the climate of the Tropical America, from where most Chinese alien flora originated. Therefore, the similarity in climate conditions between native and introduced ranges might have facilitated the introduction and establishment of alien flora in these regions. Our findings concord with the previous studies, which also identified the provinces of south, southwest, and east China as alien plant invasion hotspots in China.[32] Interestingly, introduced flora is increasingly being reported from the north and northwest provinces of China over the last 50 years, which can be attributed to the increasing ecosystem sensitivity of these regions to the climate change[45] and rapid land use changes driven by both natural and anthropogenic factors.[46]

Although the first record of the alien species may be affected by a lag time in reporting and disparity in research efforts,[39] they will persist in the country for enough time to become naturalized across different environmental conditions, add ecological and economic burdens, and increase invasion debt.[47] Indeed, China's invasive and naturalized species have significantly higher MRT than the introduced species, being similar to a previous study on the alien flora of the Azores, Czech Republic, and New Zealand.[8] Therefore, for proactive management of the alien species, it is crucial to identify the factors influencing their residence time in the country.

Abiotic factors directly influence residence time

The phylogenetically controlled structural equation modeling framework revealed that the abiotic variables could influence the residence time of alien plant species more than biological ones, thereby refuting our second hypothesis. A similar pattern was observed for the alien flora of Chile, the geographic distribution of which was more influenced by the abiotic variables than their biological characteristics.[15]

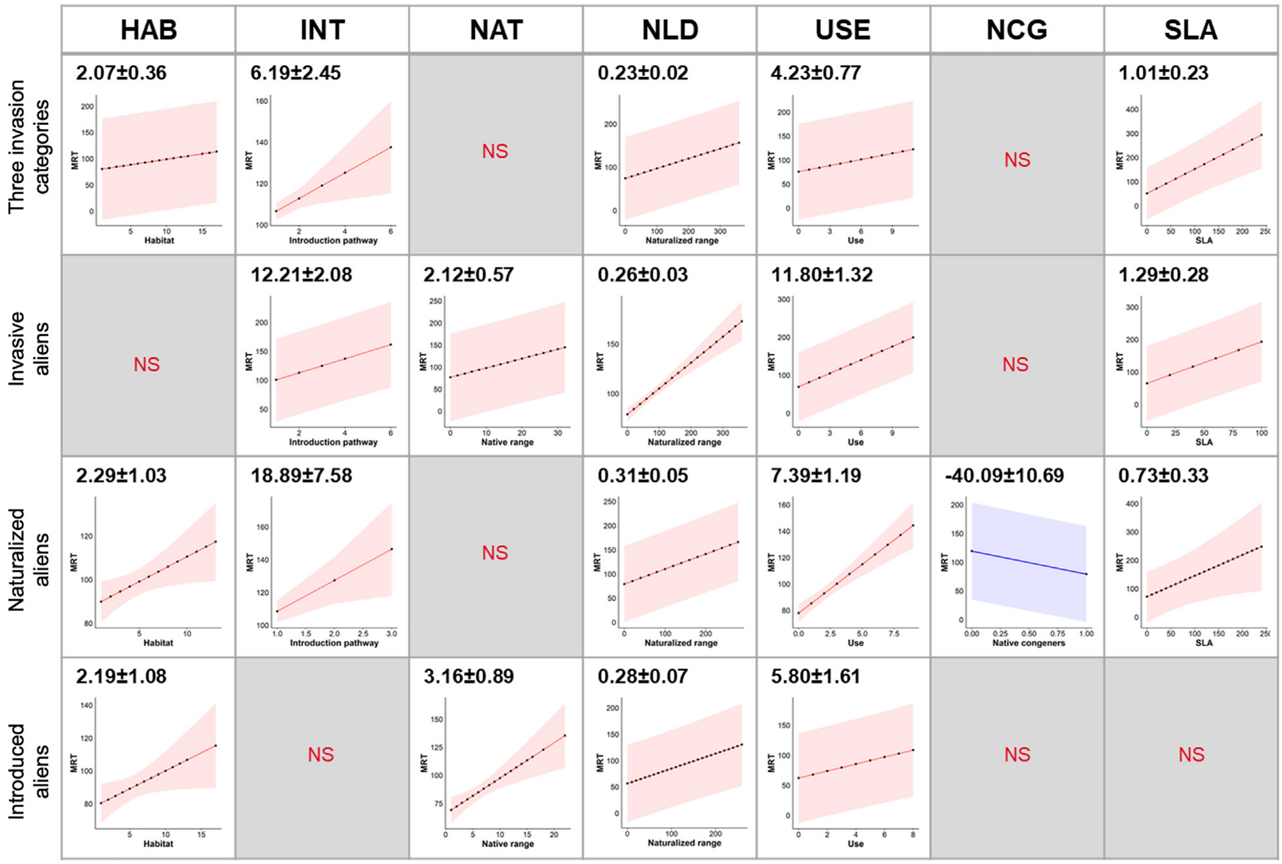

Figure 5. Relationships between the variables and MRT (minimum residence time) of the Chinese alien flora

Matrix of the phylogenetic generalized least square regression models showing the relationships between the variables and MRT (minimum residence time) of the three invasion categories together and separately. The estimate and standard error for each relationship are mentioned. Only the significant relationships at $p < 0.05$ are shown (NS indicating non-significance). Variables' codes are provided in Table 1.

Among the abiotic variables, we observed a significant and direct positive influence of the naturalized range size on the MRT of alien species across the three invasion categories. Naturalization of a species outside its native range often facilitates stepping-stone dispersal,[48] which increases the likelihood of its early introduction into a novel geographic area. Such secondary introductions and pre-adaptation to similar environments aid the introduced species in successful naturalization and invasion.[49] Based on the non-imputed data, the positive influence of the native range size on the MRT of the introduced aliens indicates that a larger source pool facilitates the early introduction of alien plant species. These findings indicate that alien species' biogeography, especially their global invasion history, influences a species' introduction time to novel geographic regions and can be an important predictor for future invasion.[50,51]

The significantly positive and direct influence of the number of uses on the MRT of alien species indicates that a large number of uses expedite the introduction of alien species and increase the likelihood of their successful naturalization and invasion. Similar impacts of uses on species invasion have been reported in many studies.[18] Our study further shows how the specific uses of alien species can influence the invasion success by modulating their introduction time. For example, China has a long history and tradition of using and importing medicinal plants, e.g., from Nepal through the trans-Himalayan medicinal plant trade, collected mainly from natural and wild resources.[52] Therefore, it was not surprising to find a positive relationship between the medicinal use and MRT of the invasive and naturalized aliens.

Apart from biogeography and uses, the direct positive relationship between the number of habitats and MRT of the introduced aliens indicates that the ability of alien species to occupy a large number of habitats, especially terrestrial and managed habitats (as evident from the LASSO regression), might facilitate their early introduction. Indeed, alien species are often favored for their large niche breadth and tolerance of a broader range of environmental conditions, which help them to occupy diverse habitats.[53] After the introduction to the terrestrial managed habitats (e.g., agricultural land, managed forests, and plantations), a subset of these species might escape from cultivation to the wild (i.e., becoming introduced aliens[7]), as "escape from confinement" was found to be the principal introduction pathway of the introduced aliens.

Indirect influence of the biotic and abiotic variables on residence time

In addition to their direct effects on the MRT of Chinese alien flora, the three abiotic variables were also influenced by other variables and could indirectly influence the MRT of the Chinese alien flora.

Table 1. Overview of the data used in this study to determine the relative importance of biotic and abiotic variables on the minimum residence time of alien plant species in China

Variables	Coded as	Data type	Levels	Ecological basis for selection
Biotic variables				
Growth form	GFM	Categorical	Three categories (Herb, Shrub, Tree)	Key determinant for introduction pathways establishment success
Native congeneric species	NCG	Discrete	Number	Increases the chance of introduction and dispersal
Specific leaf area (SLA; mm^2mg^{-1})	SLA	Continuous	Number	Functional traits are advantageous for competitive ability, important for dispersal, colonization, recruitment, and regeneration, and enhance the establishment success
Maximum height (cm)	HGT	Continuous	Number	
Seed weight (g/1,000 seeds)	SED	Continuous	Number	
Abiotic variables				
Use[a]	USE	Discrete	Number of uses (based on 50 Level-2 categories[e])	Influences introduction time, pathways, and establishment success
		Categorical	13 Level-1 categories[e]	
Habitat[b]	HAB	Discrete	Number of habitats (based on 39 TDWG Level-2 categories[e])	Determines the residence time and influences establishment ability
		Categorical	5 Level-1 categories[e]	
Native range[c]	NAT	Discrete	Size (based on the number of 52 TDWG Level-2 categories[f])	Propagule sources influence introduction time and pathways and determine successful establishment
		Categorical	8 Level-1 categories[f]	
Naturalized range[c]	NLD	Discrete	Size (based on the number of TDWG Level-4 categories[f])	
		Categorical	8 Level-1 categories[f]	
Introduction pathway[d]	INT	Discrete	Number (based on 44 Level 2 of introduction pathways[e])	Influences propagule pressure, residence time, and establishment success

[a]Plant uses are categorized following the Economic Botany Data Collection Standard.[70]
[b]Habitat information is categorized following the CABI-Invasive Species Compendium database (https://www.cabidigitallibrary.org/product/qi).
[c]The biogeographic range follows the World Geographical Scheme for Recording Plant Distributions.[71]; TDWG, International Working Group on Taxonomic Databases for Plant Sciences (TDWG); Level 1 (Continental), Level 2 (Subcontinental) and Level 4 (Political units of a country).
[d]The introduction pathways are categorized following the Convention on Biological Diversity standard.[6]
[e]Variable categories of use, habitat, and introduction pathways are mentioned in the supporting data: https://figshare.com/s/25487b8ee2551cdc6a7e.
[f]Variable categories of the native and naturalized ranges are available at https://www.tdwg.org/standards/wgsrpd/.

Positive relationships between the number of uses and naturalized range size indicate that a large number of uses increase the chances of species' dispersal to novel geographic regions, where further uses and propagule pressure help the species to become naturalized and invasive.[54] The positive relationship between native and naturalized range sizes indicates that the probability of a species becoming naturalized outside its native range was positively related to its native range size and residence time.[20,55] Finally, a positive relationship between habitats and native range size for the naturalized aliens (non-imputed data) is consistent with fitness homeostasis theory,[56] which posits that species pre-adapted to a broad range of habitat conditions in their native range are more likely to be naturalized successfully in their introduced range.[53] Overall, these findings indicate that native range size and number of uses and habitats can indirectly facilitate early introduction of alien species by increasing the naturalized range size and making a larger source pool of alien species populations.

Among the biotic variables, species' growth form and height were positively associated with the number of uses (partially imputed data) and habitats (non-imputed data) of the introduced aliens, indicating that alien tree species with many uses and broad ecological niches might have been introduced into China but did not have enough time to invade.[57] In fact, the average MRT of the introduced tree species was found to be the lowest among all growth forms and invasion categories. On the other hand, the negative relationships of these two biotic variables with biogeographic range sizes of the invasive and naturalized aliens indicate that the alien species with herbaceous growth form and shorter heights can expand their biogeographic range.[58] Besides, the herbaceous growth forms are more widely traded, less susceptible to

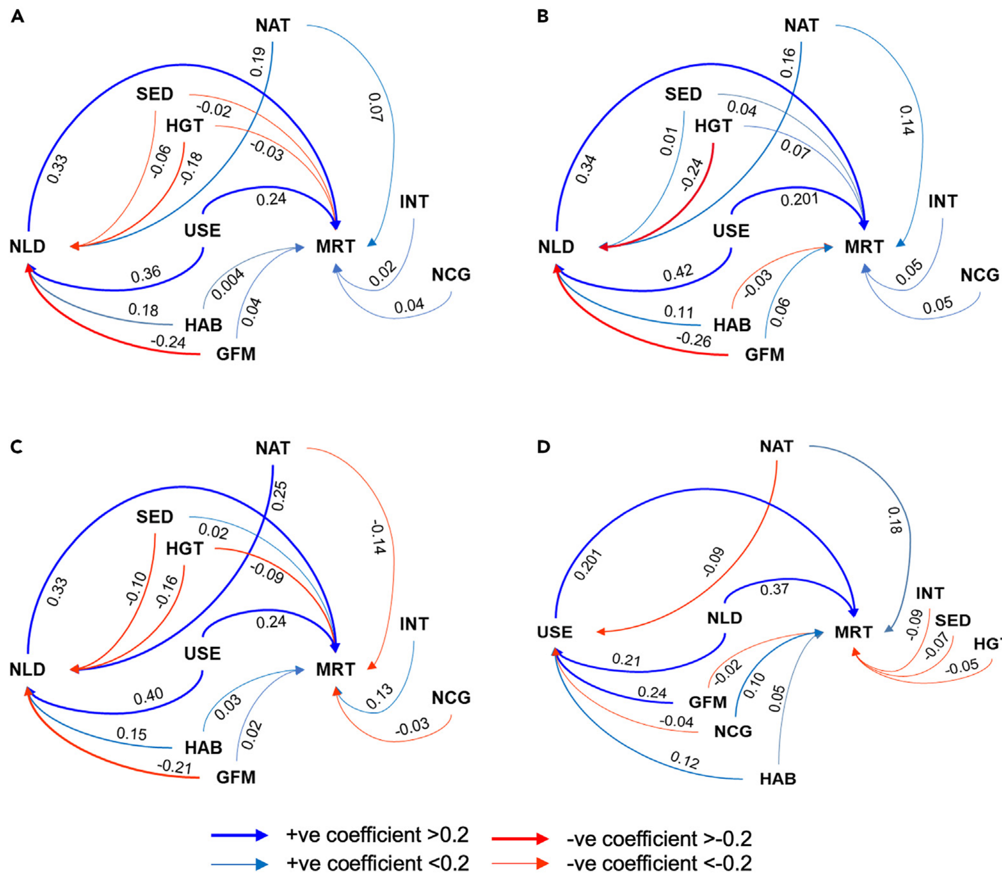

Figure 6. Direct and indirect influences of the variables on the MRT (minimum residence time) of the Chinese alien flora

Results of the phylogenetic path analysis to identify direct and indirect influences of the variables on the MRT (minimum residence time) values of – (A) three invasion categories together, (B) invasive aliens, (C) naturalized aliens, and (D) introduced aliens. The positive and negative coefficients are marked in different colors. Variables' codes are provided in Table 1.

landscape changes, require less time to adapt to environmental changes, and typically occupy broader climatic niches.[59] Therefore, larger source population and consumer preference might facilitate early introduction of alien species, as also evident for the Chinese alien flora in our study, and the increased residence time helps in successful naturalization and invasion of these species in their introduced range.

The variables' direct and indirect influences on residence time were obscured when univariate logistic regression models were used. Nevertheless, the significant positive relationship between the number of introduction pathways and MRT of invasive and naturalized aliens indicates that a greater number of introduction pathways increases the residence time of the alien species in the introduced region, which in turn increases chances of successful naturalization and invasion of alien species.[8,34] A significant positive relationship was also observed between the SLA and MRT of the invasive and naturalized aliens. SLA is often associated with a species' capacity for rapid growth and tissue turnover.[60] Species with such traits that give them growth advantage are often favored for introduction into novel geographic areas (e.g., cultivar-specific trait[61]). After the introduction, high SLA helps the species successfully invade.[62]

Management implications

The lack of saturation in alien plant species in China for the last 80 years indicates that, without modifying the current biosecurity infrastructure of the country, new alien species will continually be introduced into the country, at least for the next 20 years. Rapid globalization and ongoing climate change may further escalate new alien species introductions into the country, especially into novel areas like the north and northwest provinces, as observed in this study. Longer presence of alien species will increase their chances of successful naturalization and invasion. Therefore, early detection of alien species and implementation of scientifically informed management measures can pre-empt severe problems. In this context, the high-resolution, curated data on the MRT values of alien flora in China can be a valuable source of information for taking management actions (e.g., species with higher MRT values for prioritized management) and can address the data availability need of future research (e.g., identifying emerging invaders for proactive management measures).

Positive relationships between uses, biogeography, and MRT imply that the alien flora's unabated movement and continued uses will facilitate their early introduction to hitherto uninvaded regions. We suggest that the national policy framework includes dedicated policies for alien plant species to regulate international and domestic trading.[63] The existing quarantine measures need to be updated with a risk assessment framework, including the global invasion history of the species (e.g., biogeographic range information where the species is naturalized outside China).[64] Resources should also be leveraged to increase public awareness about the alien species, taking proactive management measures in form of early detection and rapid response, and reducing dependence on these species for socioeconomic purposes.

Finally, we observed the facilitative role of the number of introduction pathways on MRT of alien species, and the trend will continue given that rapid globalization and climate change are opening new introduction pathways for alien species,[19] e.g., the Belt and Road Initiative of China.[65] However, pathway information is lacking for many species in China, similar to, e.g., South Africa.[66] Therefore, in line with Target 6 of the CBD's Global targets for 2030 (Convention on Biological Diversity, Target 6; https://www.cbd.int/gbf/targets/6/; accessed on 30 May 2023), identification of the introduction pathway(s) associated with each alien species should be prioritized, and the information needs to be included in the national policy framework.

Limitations of the study

Our study shows for the first time at a national scale that new alien vascular plant species have accumulated in China constantly for the last 80 years. However, we have identified specific scopes of improvements that can further advance our knowledge of the invasion dynamics. First, we considered the alien plant species recorded until 2021. The availability of new information on the alien flora of China (e.g.,[67,68]) can change the current findings. Second, Global Biodiversity Information Facility (GBIF), one of the primary data sources of the first record of alien flora considered in this study, cannot adequately represent the actual distribution of the species in China.[69] Consulting literature records can further increase the resolution of the first record data of the alien flora in China. Third, most databases consulted here to curate the dataset are dynamic (e.g., GBIF and Chinese Virtual Herbarium [CVH]). Therefore, the findings of this study should be interpreted in the context of accession dates of specific data. Fourth, several factors other than the biotic and abiotic variables, e.g., land use, biodiversity of the recipient community, and the pathways and vectors of introduction, may also influence the residence time of the alien flora. Therefore, considering the spatiotemporal information on these variables in future studies will provide deeper insights into the invasion dynamics. Finally, increased data resolution of certain biotic (e.g., SLA) and abiotic (e.g., introduction pathway) variables can also change the relative influence of the variables on the alien species' residence time. The findings of the study can be enhanced further by data collected from long-term field experiments and monitoring studies.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2024.109552.

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AUTHOR CONTRIBUTIONS

Conceptualization, A.K.B. and Y.H.; methodology, A.K.B. and A.R.B.; data curation, H.F., X.L., M.Y., H.P., and F.D.; formal analysis, A.K.B. and A.R.B.; investigation, A.K.B., Y.Y., and Y.H.; writing – original draft, A.K.B.; writing – review and editing, Y.Y. and Y.H.; visualization, A.K.B., H.F., and A.R.B.; resources, Y.H.; supervision, A.K.B. and Y.H.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Information of alien plant species used in this study	Figshare	https://figshare.com/s/25487b8ee2551cdc6a7e (https://doi.org/10.6084/m9.figshare.23806170)
List of alien plant species in China	Naturalized alien plants of China	https://doi.org/10.1007/s10531-011-0044-x
List of alien plant species in China	Ma and Li[72]	List of Invasive Alien Plants in China - Baidu Academic
List of alien plant species in China	Global Register of Introduced and Invasive Species (GRIIS) - China Version 1.3	https://www.gbif.org/dataset/6d11211b-caa0-4e63-b99c-e944099d5017
Taxonomic standardization of species names	World Flora Online (WFO) taxonomic backbone data	https://about.worldfloraonline.org/
Origin status of alien plant species in China	Plants of the World Online (POWO)	https://powo.science.kew.org/(20 February 2022)
Origin status of alien plant species in China	Germplasm Resources Information Network (GRIN)	https://www.ars-grin.gov/(20 February 2022)
Residence status of alien plant species in China	Global Biodiversity Information Facility (GBIF)	http://www.gbif.org (19 October 2023)
Residence status of alien plant species in China	Chinese Virtual Herbarium (CVH)	https://www.cvh.ac.cn/(19 October 2023)
Residence status of alien plant species in China	Seebens et al.[5]	Global Alien Species First Record Database version 1.2 https://doi.org/10.1038/ncomms14435
Residence status of alien plant species in China	Xu et al.[33]	https://doi.org/10.3897/neobiota.15.3575
Residence status of alien plant species in China	Ding et al.[73]	https://doi.org/10.1641/B580407
Growth form of alien plant species in China	TRY Plant Traits Database	https://www.try-db.org/TryWeb/Home.php (19-20 October 2023)
Functional traits of alien plant species in China	TRY Plant Traits Database	https://www.try-db.org/TryWeb/Home.php (20-27 October 2023)
Functional traits of alien plant species in China	Literature reports from ISI Web of Science	https://webofknowledge.com/ (20-27 October 2023)
Native congeneric species of alien plant species in China	List of plant species in China (2022 edition)	https://www.plantplus.cn/doi/10.12282/plantdata.0061 (11 October 2023)
Native congeneric species of alien plant species in China	Germplasm Resources Information Network (GRIN)	https://www.ars-grin.gov/ (19 October 2023)
Use of alien plant species in China	Scientific Database of China Plant Species	http://db.kib.ac.cn/Default.aspx (20 October 2023)
Use of alien plant species in China	Germplasm Resources Information Network (GRIN)	https://www.ars-grin.gov/ (21-27 October 2023)
Use of alien plant species in China	CABI Invasive Species Compendium	https://www.cabidigitallibrary.org/product/qi (21-27 October 2023)
Use of alien plant species in China	Useful Tropical Plants database	http://tropical.theferns.info/ (21-27 October 2023)
Use of alien plant species in China	Useful Temperate Plants database	http://temperate.theferns.info/ (21-27 October 2023)

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Continued

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Habitat of alien plant species in China	CABI Invasive Species Compendium	https://www.cabidigitallibrary.org/product/qi (22-25 October 2023)
Native range of alien plant species in China	Plants of the World Online (POWO)	https://powo.science.kew.org/ (19-23 October 2023)
Native range of alien plant species in China	Germplasm Resources Information Network (GRIN)	https://www.ars-grin.gov/ (19-23 October 2023)
Naturalized range of alien plant species in China	Global Naturalized Alien Flora (GloNAF) database	https://doi.org/10.1002/ecy.2542
Introduction pathway of alien plant species in China	Advanced search function of the Google Scholar database	https://scholar.google.com/#d=gs_asd (19-25 October 2023)
Introduction pathway of alien plant species in China	CABI Invasive Species Compendium	https://www.cabidigitallibrary.org/product/qi (25 October 2023)
Introduction pathway of alien plant species in China	Literature reports from ISI Web of Science	https://webofknowledge.com/ (26-27 October 2023)
R code (and data) used for data analysis	Figshare	https://doi.org/10.6084/m9.figshare.23806170
Software and algorithms		
R version 4.0.2	R Core Team[5]	https://www.R-project.org/
Interactive Tree Of Life version 3.0	Letunic and Bork[74]	https://itol.embl.de/(20 October 2023)

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Yelin Huang (lsshyl@mail.sysu.edu.cn).

Materials availability

The dataset of the alien species' residence time is provided as a private-for-peer review via the following link: https://figshare.com/s/25487b8ee2551cdc6a7e (https://doi.org/10.6084/m9.figshare.23806170).

Data and code availability

- The R codes are deposited at Figshare and is publicly available as of the date of publication. The DOI is listed in the key resources table.
- Species information and data associated required to run the R codes are deposited at Figshare and are publicly available as of the date of publication. The DOI is listed in the key resources table.
- Any additional information required to reanalyze the data reported in this work paper is available from the lead contact upon request.

METHOD DETAILS

Species list preparation and data collection

We first created a comprehensive list of alien plant species in China by consulting three nationwide checklists published until 2021, viz. naturalized alien plants of China [n = 861;[75]], The Checklist of the Alien Invasive Plants in China [n = 464;[72]], and the Global Register of Introduced and Invasive Species (GRIIS) - China Version 1.3 [n = 459;[76]]. The data sources provided authentic and comprehensive lists of alien plant species in China with traceable data sources. To remove ambiguity and orthographical errors in the plant nomenclature, automated standardization of taxonomic names was conducted using the WorldFlora package[77] in R version 4.0.2[78] (hereafter, R). This package validates the species names against a static version of the World Flora Online (WFO) taxonomic backbone data, which is actively curated by global experts based on The PlantList backbone (http://www.theplantlist.org/) and therefore provides the most updated and comprehensive taxonomic reference of vascular plants.[79] The list was further cleaned by removing duplicates and synonyms, and the infraspecific taxa and artificially hybridized species were not considered further (Figure S1).

For each species (n = 912), we assessed the origin status (the species is either native or alien to China), invasion status (the degree of naturalization of the species), and residence status (earliest year of the species record) (sensu[80]). The origin and invasion status were determined based on a consensus approach of the three above checklists and two global databases (details in Note S1). The oldest occurrence record of the species in the country was retrieved from – 1) the Global Biodiversity Information Facility (http://www.gbif.org; accessed on 19 October 2023), 2) the Chinese Virtual Herbarium (https://www.cvh.ac.cn/; accessed on 19 October 2023), 3) the Global Alien Species First Record

Database version 1.2 [5], and two literature reports.[33,73] We considered the earliest year recorded among the five sources to assess the residence status of the species in China. We did not consider records prior to 1840 (ancient China). The minimum residence time (MRT, hereafter) was calculated by subtracting the earliest recorded year from the year of the study (2022). Finally, we got a list of 721 alien plant species belonging to three invasion categories: introduced (i.e., individuals outside of cultivation but incapable of surviving for a significant period; n = 173), naturalized (i.e., individuals surviving outside of cultivation with a self-sustaining population; n = 247), and invasive (i.e., self-sustaining population outside of cultivation with individuals dispersing, surviving, and reproducing across multiple habitats, and negatively impacting biodiversity, ecosystem service and human well-being; n = 301) (Figure S1).

For each 721 species, we collected data on ten biotic and abiotic variables that can potentially influence the MRT [Table 1]. Among the biotic variables, we considered – 1) growth form, 2) three functional plant traits, and 3) native congeneric species. Five abiotic variables were considered – 1) use, 2) habitat, 3) native range, 4) naturalized range, and 5) introduction pathway (Figure S1). The detailed process of data extraction and validation is provided in Note S1.

In addition, the geographic coordinates of the first recorded observations were also collected. Among the five data sources we considered in this study, geographic coordinates (latitude and longitude) were available only for the GBIF records. The locality descriptions from other data sources were used in the Google Earth Pro Desktop version (https://www.google.com/earth/versions/#earth-pro) to georeference occurrence data lacking geographic coordinates at a precision level of two decimal degrees. In cases where location information was too vague or in large geographic areas (e.g., province name), the described polygon's centroid was used to define the coordinates. If the earliest record date among the five data sources had – i) missing location information and/or coordinates and/or ii) only the country name mentioned as location information, we considered the second earliest record date of the species and collected the corresponding geographic coordinates. At the end of this exercise, we obtained geographic coordinates of the first record for 576 species.

The quality of the collected data (species identity, earliest record, variable information, and geographic coordinates) was assessed using a checklist with three criteria – reliability, usability, and accessibility (details provided in Note S1). Each data was extracted from highly cited and well-regarded databases, peer-reviewed authoritative scientific journals, and published books. Therefore, the curated data should be considered as reliable and consistent. Moreover, each data was provided with traceable data sources to increase the reliability of the dataset. Technical validation of the curated data was performed by random and iterative data checking by individual team members to minimize the curator's bias, avoid omission errors, and increase the data accuracy. The dataset was provided as supplementary material without restriction to ensure smooth usability and accessibility.

QUANTIFICATION AND STATISTICAL ANALYSIS

Analysis of spatiotemporal trend

We used the yearly number of species (first record rate, hereafter) from 1840 to 2020 to analyze the temporal trend. We fitted five functions to the time series data: linear $y = a + bx$, exponential $y = ae^{bx}$, saturating $y = a(1 - e^{-bx})$, hyperbolic $y = \frac{ax}{x+b}$, and sigmoidal $y = \frac{ax^2}{x^2+b^2}$, where y = first record rate, x = time, and a, b are constants. The five functions were selected to test whether – 1) the temporal trends in the first record rate can be captured by these functions, and 2) the fitting of these functions provided different first record rate pattern from that observed at the global scale.[5] The functions were fitted using the Gauss-Newton optimization algorithm implemented in the 'nls' function in R. Akaike's Information Criterion of each fitting was used to identify the function that could best describe the time series of the first record rate. To check for the effect of the outliers on function fitting, we fitted the functions with and without the outliers of the data.

We used segmented regression to test for a potential increase or decrease of the first record rate in recent years. A segmented relationship is defined by the slope parameters and the breakpoints where the linear relationship between the response and explanatory variables changes. A linear regression model was fitted with segmented relationships between the first record rate (response variable) and year (explanatory variable). We specified the initial value as 1900 to estimate the breakpoints. Linear regression models were then fitted with the post-breakpoint ($\pm$2 standard errors) data to identify the increasing or decreasing trend of the first record rate.

We further assessed the temporal trend of the first record rate of the alien plant species in the future. We identified the year when the first record rate became stabilized and simulated 1000 bootstrap first record rate data between the stabilized time point and 2020. Linear regression models were then fitted on the simulated data, and the prediction values of the first record rate were obtained for 2030 and 2040. The histograms of the 1000 predicted values were approximated by the kernel density and normal density functions to identify the average of predicted first records.

Using ArcMap version 10.2, we mapped the distribution of the first records of the alien plant species at the provincial level. The analyses were conducted for all alien species and three invasion categories separately. The mapping was done for three time periods: earliest record date to 1920 (first 80 years covering the breakpoints of all alien species and the three categories), 1921–1970 (next 50 years covering the breakpoints $\pm$5 standard errors of all alien species and the three categories), and 1971–2020 (last 50 years covering the breakpoints $\pm$10 standard errors of all alien species and the three categories).

Comparative analysis

The MRT values were compared between the three invasion categories of alien species, with and without considering the categorical variables [first-level categories of the biotic and abiotic variables (Table 1)]. As the data did not comply with the assumptions of normality and homogeneity of variance, we used the non-parametric alternatives for one-way ANOVA (Kruskal-Wallis H and posthoc Dunn's test when the invasion categories were considered) and two-way ANOVA [aligned ranks transformation (ART) ANOVA test when both the invasion and variables categories were considered] for these analyses. The p values in all comparative analyses were adjusted with the Holm method for multiple comparisons.

Identifying variables' influence on MRT

After accounting for phylogenetic signals, we identified the variables' influence on the MRT by univariate and multivariate regression models. The presence of phylogenetic signals was ascertained based on the significant difference between the observed and randomized estimates of two metrics - Blomberg's K and Pagel's λ (details provided in Note S2). For univariate regression, we used logistic regression for variables with no phylogenetic signals and phylogenetic generalized least square (PGLS) regression (assuming the Brownian motion model of evolution) for variables with phylogenetic signals. The categorical growth form variable ($K = 3$) was coded as three ($K-1$) dummy variables.

Multivariate regression analysis was performed to decipher the direct and indirect relationships among variables and their influences on the MRT through phylogenetic path analysis (PPA). Imputation of missing values (Figure 1B) was conducted for six variables with <50% missing data (except for specific leaf area) using a non-parametric iterative method (with 100 iterations) based on the random forest algorithm. The plant traits were standardized for each growth form. We then established a set of six PPA models considering the hypothesized relationships between the variables (Note S2). The path analysis was conducted based on Pagel's λ model of evolution. The fitted models were evaluated based on the C-statistic values, and the significant models were averaged to fit the final model. The regression coefficients for the absent paths were set to zero to facilitate the detection of weak effects and avoid biases associated with coefficients away from zero. Path analysis was also done on the subset of species with complete data.

The PPA models revealed direct effects of the naturalized range size, number of uses, and habitats on the MRT of the alien species (see results). Therefore, we used the LASSO (least absolute shrinkage and selection operator) regression analysis to identify the categories of naturalized range, uses, and habitats that can influence the MRT. The number of naturalized ranges for each of the nine continents, the number of uses for each of the 13 categories of uses, and the number of habitats for each of the six categories were used as explanatory variables, whereas the MRT values were considered the response variable. The important variables were chosen by using the cross-validated LASSO regularization method.

The analysis of temporal trends and identification of variables' influence on MRT were conducted considering the three invasion categories (i.e., invasive, naturalized, introduced) together and individually. All statistical analyses were performed in R; the details are provided in Note S2.