

Article

Drivers of Species Distribution and Niche Dynamics for Ornamental Plants Originating at Different Latitudes

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Abstract: Human activities provide migration opportunities for many ornamental plants and make them become a new potential invasion risk, threatening the local ecosystem. However, ornamental plants come from a wide range of sources, and there is still a lack of understanding on the distribution driving factors, ecological niche dynamics and invasion ability of ornamental plants based on the origin of different latitudes to evaluate their potential invasion risks. In this study, an ensemble of ecological niche model and a niche dynamic model were used to analyze the invasion potential of herbaceous and woody ornamental plants originating from different latitudes. The results showed that there were significant differences in environmental factors driving the distribution of plants originating from different latitudes, and climate-related factors were the primary driving force for each plant in the native and introduced regions. Urban land was the most influential factor in the introduced areas of most plants, potentially reflecting the importance of human activities in the distribution of ornamental plants. Additionally, only woody plants originating from mid-latitudes showed greater diffusivity than those originating in high latitudes and low latitudes, and the niche widths of all the herbaceous plants in the introduced regions nearly exceeded those in the native regions. This phenomenon was observed only in woody plants with mid-latitude origins. The niche similarity of all plant species between the introduced and native regions was high, indicating that all species in the introduced regions inherited niche characteristics from plants in the native regions.

Keywords: ornamental plants; distribution driving factors; niche dynamics; niche conservatism; biological invasion



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1. Introduction

Biodiversity has always been strongly affected by human activities, and species invasion caused by humans is a serious threat to biodiversity [1,2]. People are aware of the harm to native ecosystems caused by invasive species, and many measures have been taken to control the invasion of alien species. However, there are still some human activities that actively introduce species into new areas, such as agricultural activities, to obtain economic benefits. Currently, the number of alien plants escaping from cultivation into native ecosystems is steadily increasing [3]. Food crops (especially staple crops that are necessary for human survival and development) are strongly dependent on human care in the long process of cultivation and lack competitive and invasive ability in the wild, while ornamental plants are thought to retain more invasive ability in the wild. Studies indicated that most ornamental alien plants have been introduced intentionally in public and private gardens and have become a new potential invasion risk, affecting local ecosystems [3,4]. Therefore, understanding the potential invasion mechanisms of ornamental plants as invasive species is particularly important for ecosystem protection.

There are abundant sources of popular ornamental plants originating from different latitudes, and the climate zones formed by different latitudes are usually considered to play a key role in the distribution and dispersal of species [5]. On the one hand, the climate determined by geographical clines is a strong selective factor for plant traits, determining the ability of native species to adapt to the environment [6]. On the other hand, both colonization and invasion success along broad environmental gradients may be partially due to phenotypic plasticity to adapt to specific environments [7]. Plants originating from low latitude regions often have richer survival strategies and competitive potential but are highly dependent on high or moderate temperatures and abundant water [8]. Plants originating in high latitudes usually have more conservative survival strategies due to the relatively harsh living environment [9]. Although humans promoted the initial establishment of nonnative species, the spread and subsequent distribution of nonnative species are largely the result of their own genetic characteristics interacting with biological and environmental factors [10,11]. Ornamental plants originating from different latitudes have significant differences in their plant traits and environmental adaptation strategies due to the influence of climate conditions on their origins, and the differences in these traits or strategies will provide basis for the possibility of ornamental plants living in new areas. However, few studies have discussed the invasion potential of species from different latitudes based on their origin [12], and it is still unknown whether there are differences in the environmental driving factors affecting the distribution and dispersal of ornamental plants originating from different latitudes.

As an important concept connecting ecology and biogeography, the ecological niche plays an important role in understanding the mechanism of spatial and temporal distribution patterns of species [13]. Human activities can take species to areas beyond their original ranges, giving the species the opportunity to adapt to new environments, shifting its niche spaces and colonizing in new regions [14]. However, there are many controversies about the niche conservatism of species, and studies also showed that substantial niche shifts are rare among terrestrial plant invaders [15]. For ornamental plants, human preference provides many opportunities for their dispersal. When they enter the introduction site from their original place, they will adjust their survival strategies to adapt to the new environment. However, little is known about whether their ecological niche will shift in this process, especially when these ornamental plants originate from different latitudes. Therefore, exploring the ecological niche dynamics and the invasion ability reflected in this process of ornamental plants based on their origin is particularly important for understanding invasion mechanisms and can also help us evaluate the potential impacts and risks of ornamental plants from different regions on local ecosystems following introductions.

Plants chosen for ornamental purposes are not randomly selected [3]. At present, global trade and economic and social development needs also provide many opportunities for ornamental plant invasion [16–18], so it is necessary to establish a scientific regulatory framework to monitor invasive ornamental plants. Species invasion results from adaptation to potential habitats and shifts in niches [14,19], so a greater understanding of the ecological factors affecting species invasion and niche shifts can be used to further explore the invasion mechanisms of ornamental plants at a global scale. In this study, an ensemble of ecological niche models was used to analyze the ecological factors that determine the potential distributions of ornamental plants originating from different latitudes, and niche dynamic models were used to analyze whether the niches of ornamental plants shifted from native to introduced regions. Considering that ornamental plants can be planted in artificial facilities, this study distinguished herbaceous and woody ornamental plants (woody plants are usually tall, and it is more difficult to house them in facilities with artificial environmental conditions) to further verify the role of ornamental plants from different latitudes in the potential invasion risk in introduced ecosystems. In this study, the following hypothesis will be verified: (1) there are differences in environmental factors driving the distribution of ornamental plants originating from different latitudes; (2) during the process from the

naive to the introduced area, there are differences in the ecological niche dynamics and invasion ability of ornamental plants of different latitude origins.

2. Materials and Methods

2.1. Occurrence Records of Plant Species with Different Latitudinal Origins

In this study, 18 plant species of different latitudinal origins were selected, of which 9 species were herbaceous and the other half were woody (Figure 1 and Table S1). The occurrence records of the 18 species were obtained from the Global Biodiversity Information Facility (GBIF) and specimen records with clear coordinates, and duplicate records were deleted. Spatial bias caused by the spatial autocorrelation of occurrence records may affect the performance of ensembles of ecological niche models (ENMs) [20]. We spatially rarefied occurrence data (SROD) with a resolution of 20 km through SDM toolboxes developed by Brown (2014) and Brown et al. (2017) to reduce the effect of spatial bias associated with having one record per grid cell [21,22], as suggested by Warren and Seifert (2011) [20]. The latitudinal distribution ranges of the origin areas of each species after data screening are shown in Figure 1. For species selection, following criteria were considered: (1) The selected species are widely recognized ornamental plants worldwide; (2) the selected ornamental plants need to originate from different latitudes, and this origin can be verified from reliable literature; (3) the number and reliability of the selected species' distribution records meet the model construction.

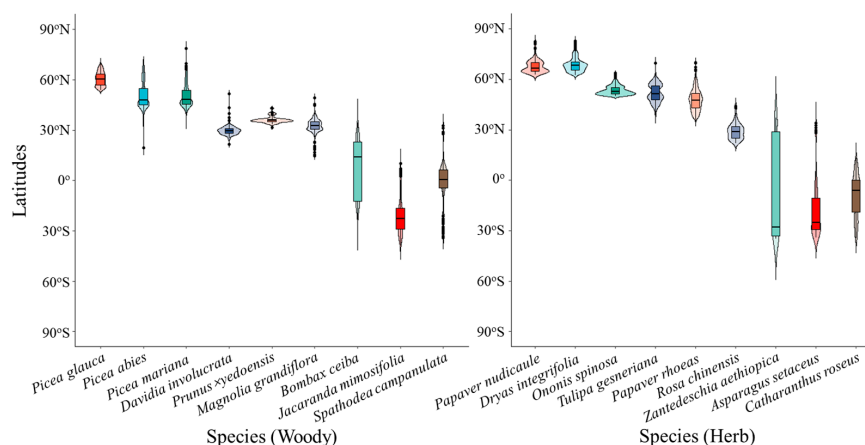


Figure 1. Latitudinal distributions of the native range of each species.

2.2. Environmental Parameters

The following predictors were used in this study: climate, land use, topographical factors, and soil factors. We used 2.5 arc minute (approximately 5×5 km) bioclimatic data for the baseline period as the climatic input of the species distribution models. We obtained the 19 baseline bioclimatic factors from WorldClim (www.worldclim.com, accessed on 1 February 2023) [23]. We obtained the 8 land-use variables considered in this study from the land-use harmonization strategy website (luh.umd.edu, accessed on 1 February 2023); the variables included forested primary land (Primf), nonforested primary land (Primn), potentially forested secondary land (Secdf), potentially nonforested secondary land (Secdn), managed pasture (Pastr), rangeland (Range), urban land (Urban), and crop land (Crop). We chose elevation, slope, and aspect as the topographical factors in this study. Elevation was determined via a digital elevation model (DEM) at a spatial resolution of 30'' (approximately 1×1 km). We derived slope and aspect from the DEM. We retrieved the 16 soil variables considered in this study from the Harmonized World Soil Database v 1.2 (<https://www.fao.org/soils-portal/data-hub/soil-maps-and-databases/harmonized-world-soil-database-v12/en>, accessed on 1 February 2023), and these variables included reference soil depth (Refdepth), available water capacity range (Awcclass), drainage class (Drainage), topsoil texture (Ttexture), topsoil gravel content (Tgravel), topsoil organic

carbon (Toc), topsoil clay fraction (Tclay), topsoil sand fraction (Tsand), topsoil silt fraction (Tsilt), topsoil reference bulk density (Tbulkdensity), topsoil pH (H₂O) (TpH), topsoil sodicity (ESP) (Tesp), topsoil salinity (Elco) (Tece), topsoil cation exchange capacity (Tcec), topsoil total exchangeable base (Tteb), and topsoil base saturation (Tbs) [24]. Moreover, to ensure a consistent resolution among the climatic predictors, we resampled all the factors listed above to a 2.5 arc-minute (approximately 5 × 5 km) grid.

2.3. Species Distribution Model

We constructed the ensemble species distribution model using the biomod2 package (4.2-3) in R, which comprised seven models, including a generalized linear model (GLM), generalized boosting model (GBM), classification tree analysis (CTA), artificial neural network (ANN), flexible discriminant analysis (FDA), random forest (RF), and MaxEnt [25]. To meet the model requirements, we set the number of pseudo absences to 1000. We established a preliminary species distribution model and obtained the importance values of all variables. Strong collinearity between variables may lead to overprediction by a model, so variables with Pearson correlation coefficients greater than 0.7 were considered to have a strong correlation. Then, the less important factors (with low importance values) were removed [26]. We repeated this process until the remaining factors did not have strong collinearity.

The remaining factors were used to build the species distribution model on the biomod2 platform. To ensure the reliability of the model, we retained the model with true skill statistics (TSS) greater than 0.7 and an area under the ROC curve (AUC) greater than 0.8. We used 70% of the data to calibrate the model and the remaining 30% for model validation. We calculated three different model evaluation indicators to evaluate the baseline model: TSS, ROC, and the kappa coefficient. Generally, TSS > 0.7, AUC > 0.8 and kappa > 0.6 are thought to indicate good reliability [27]. We used a maximum training sensitivity plus specificity (MSS) logistic threshold to distinguish the suitable and unsuitable habitats in the model.

2.4. Niche Model

To study whether the niche of species was conservative, we selected the factors that remained after removing those with strong collinearity as the independent variables, and we applied the “ecospat” package in R to analyze the niche of each species [28]. According to the time and location of the records, we defined the occurrence records from the locations where the species originated as the native occurrence records and defined the other occurrence records as the introduced occurrence records. Using the R package “ecospat”, we conducted niche equivalence and niche similarity tests and ultimately obtained the values representing niche changes, including niche breadth in the native range (BN), niche breadth in the introduced range (BI), niche expansion (E), niche stability (S), and niche unfilling (U). We used the E, S and U values to analyze the niche changes for each species. Then, we used the ln-transformed ratio of the niche breadth in the native range to that in the introduced range ($BR = \ln(BN/BI)$) to measure the changes in niche breadth and used Sørensen’s similarity index ($Sim = 2S/(BN + BI)$) to measure the changes in niche position. Following Pearman et al. (2008) and Liu et al. (2020) [26,29], the niche conservatism hypothesis will be rejected if $BR < 0$, and following Broennimann et al. (2007) and Liu et al. (2020) [26,30], the niche conservatism hypothesis will be rejected if $Sim < 0.5$. In this study, when the niche conservatism hypotheses of BR and Sim were both rejected, we concluded that the niches of the species were not conserved.

3. Results

3.1. Factors Influencing the Distributions of Plants from Different Latitudes

The importance values of the variables determining the spatial distributions of all plants in native and introduced areas from different latitudes are shown in Table S2, and the three most important factors affecting the distributions of each species are shown in

Figure 2. The three most influential factors affecting the distribution of each species in the native and introduced areas were assigned 3, 2, and 1 points, and the chi-square test was used to statistically test the environmental and latitude variables (Table S3). The results showed that there were significant differences in environmental variables affecting plants from different latitudes, whether they were native or introduced (Table S3). For species originating at high latitudes, annual temperature (BIO1) was the most important factor influencing the distribution of woody and herbaceous species in both their native and introduced areas (Figure 2A–D, Table S3). For plants originating in mid-latitudes, the most important factor influencing the distribution of woody native species was precipitation of the warmest quarter (BIO18), and the most important factor affecting the distribution of herbaceous native species was precipitation seasonality (BIO15) (Figure 2E,G, Table S3). For herbaceous and woody plants from mid-latitudes, urban land was the most important factor affecting the distributions in their introduced regions (Figure 2F,H, Table S3). For plants of low-latitude origin, temperature seasonality (BIO4) was the most important factor affecting the distributions of herbaceous native plants, while isothermality (BIO3) was the most important factor affecting the distributions of woody native plants (Figure 2I,K, Table S3). The main factor affecting the distributions of woody and herbaceous introduced plants from low latitudes was urban land (Figure 2J,L, Table S3), which was consistent with the plants of mid-latitude origin in the introduced regions.

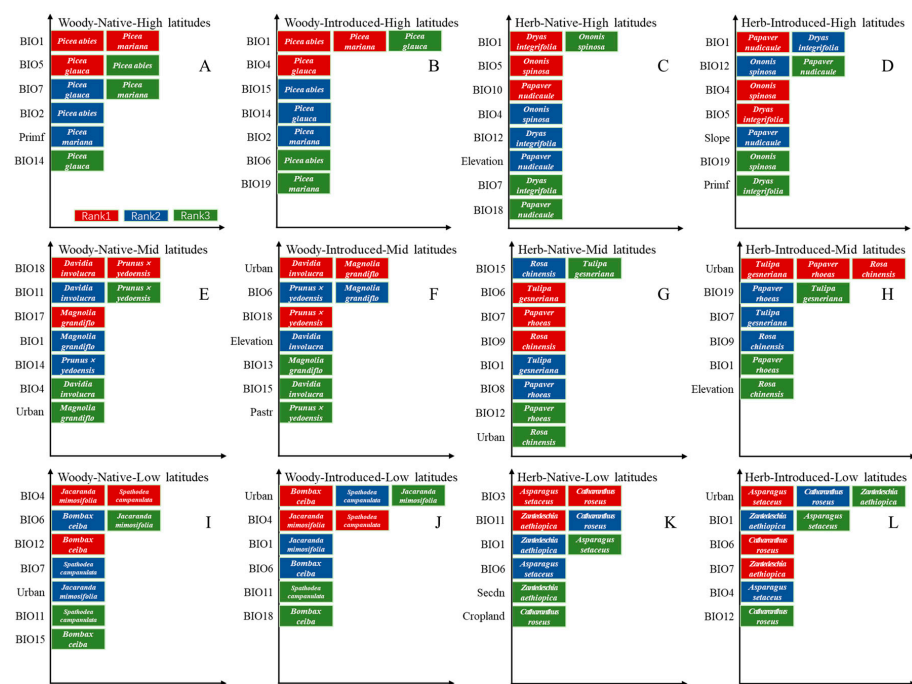


Figure 2. The driving factors of the distributions of ornamental plants originating from different latitudes in their native and introduced regions. The boxes contain the names of each species, red represents the most important driving factor affecting each species, blue represents the second most influential factor, and green represents the third most influential factor. The differences were tested statistically by the chi-square test in Table S3. (A) woody native plants originating from high latitudes; (B) woody introduced plants originating from high latitudes; (C) herbaceous native plants originating from high latitudes; (D) herbaceous introduced plants originating from high latitudes; (E) woody native plants originating from mid latitudes; (F) woody introduced plants originating from mid latitudes; (G) herbaceous native plants originating from mid latitudes; (H) herbaceous introduced plants originating from mid latitudes; (I) woody native plants originating from low latitudes; (J) woody introduced plants originating from low latitudes; (K) herbaceous native plants originating from low latitudes; (L) herbaceous introduced plants originating from low latitudes.

In this study, the three most influential factors affecting the distribution of each species in the native and introduced areas were assigned 3, 2, and 1 point, respectively (the factors were normalized, and their dynamic changes were compared, Figure 3). The key factors affecting the distributions of woody plants originating at high latitudes were highly related to temperature in both the native and introduced sites. The influences of max temperature of warmest month (BIO5) and temperature annual range (BIO7) in the introduced sites were weaker than those in the native areas, while the influences of annual mean temperature (BIO1) and temperature seasonality (BIO4) were increased (Figure 3A). For woody plants from mid-latitudes, precipitation of warmest quarter (BIO18) was the most influential factor in the native regions, while the most influential factor in the introduced regions was urban land (Figure 3B). For woody plants from low latitudes, temperature-related factors, such as temperature seasonality (BIO4) and min temperature of coldest month (BIO6), had a great influence in both the native and introduced areas, and urban land was the other highly influential factor in the introduced areas (Figure 3C). Among herbaceous ornamental plants, the most influential factors for plants originating at high latitudes changed from a precipitation-related factor [annual precipitation (BIO12)] to a temperature-related factor [annual mean temperature (BIO1) and temperature seasonality (BIO4)] from the native sites to the introduced sites (Figure 3D). For the herbaceous plants from middle and low latitudes, the factors affecting the distributions changed greatly from temperature-related factors to urban land from their native sites to their introduced sites (Figure 3E,F).

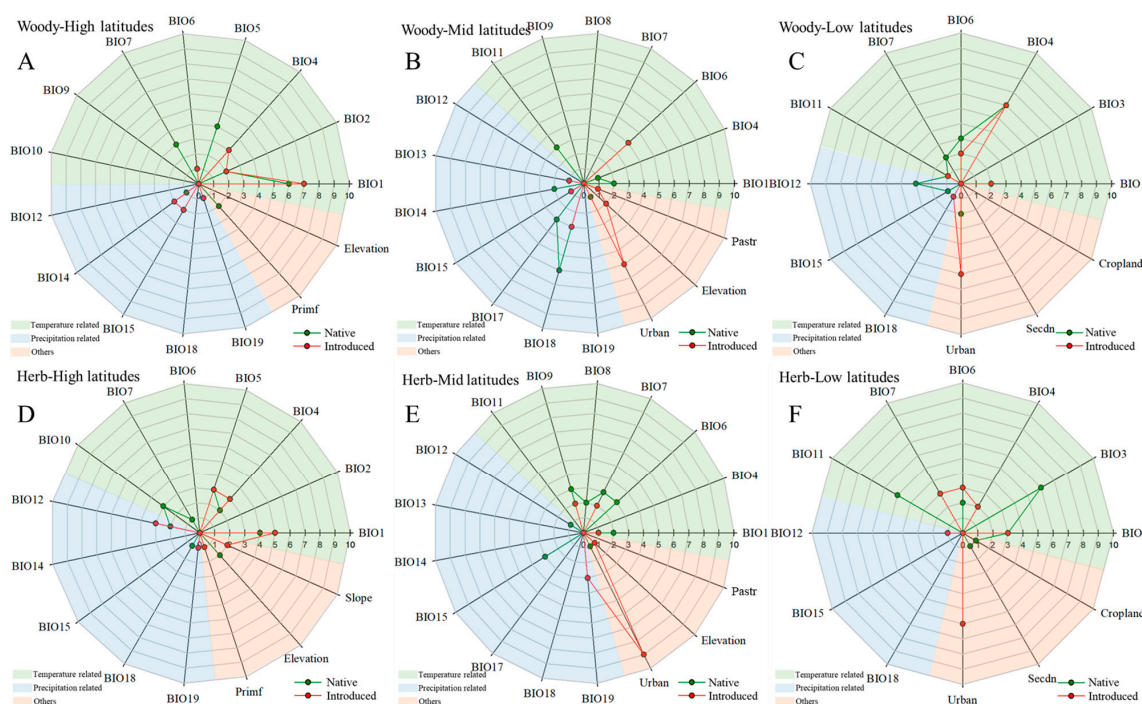


Figure 3. The cumulative scores of driving factors for ornamental plants originating from different latitudes in their native and introduced regions; green indicates temperature-related traits, blue indicates rainfall-related traits, and orange indicates other factors. (A) woody plants originating from high latitudes; (B) woody plants originating from mid latitudes; (C) woody plants originating from low latitudes; (D) herbaceous plants originating from high latitudes; (E) herbaceous plants originating from mid latitudes; (F) herbaceous plants originating from low latitudes.

3.2. Changes in Niche Space Occupied by Ornamental Plants from Native to Introduced Regions

The niche space occupied by species was divided into expansion (E), stable (S), and unfilled (U) areas. The results showed that the E values of woody plants originating from high and low latitudes were relatively small overall, with mean values of 0.049 and 0.071, respectively. These values were significantly lower than those of mid-latitude woody

plants, with a mean value of 0.234 (Figure 4A). For herbaceous plants, the E values of plants originating from different latitudes were relatively higher than those of woody plants, but there was no significant difference among them (Figure 4B). For woody plants, the S values of plants originating in the mid-latitudes (0.766) were significantly lower than those originating in the high and low latitudes (0.951 and 0.929, respectively), while there was no significant difference in S values among herbaceous plants originating in different latitudes (Figure 4C,D). The U value of woody plants showed a gradual decrease from high latitudes to low latitudes, but there was no significant difference in the value (Figure 4E). The same trend was observed for herbaceous plants, but the U value of woody plants was much higher than that of herbaceous plants (Figure 4F).

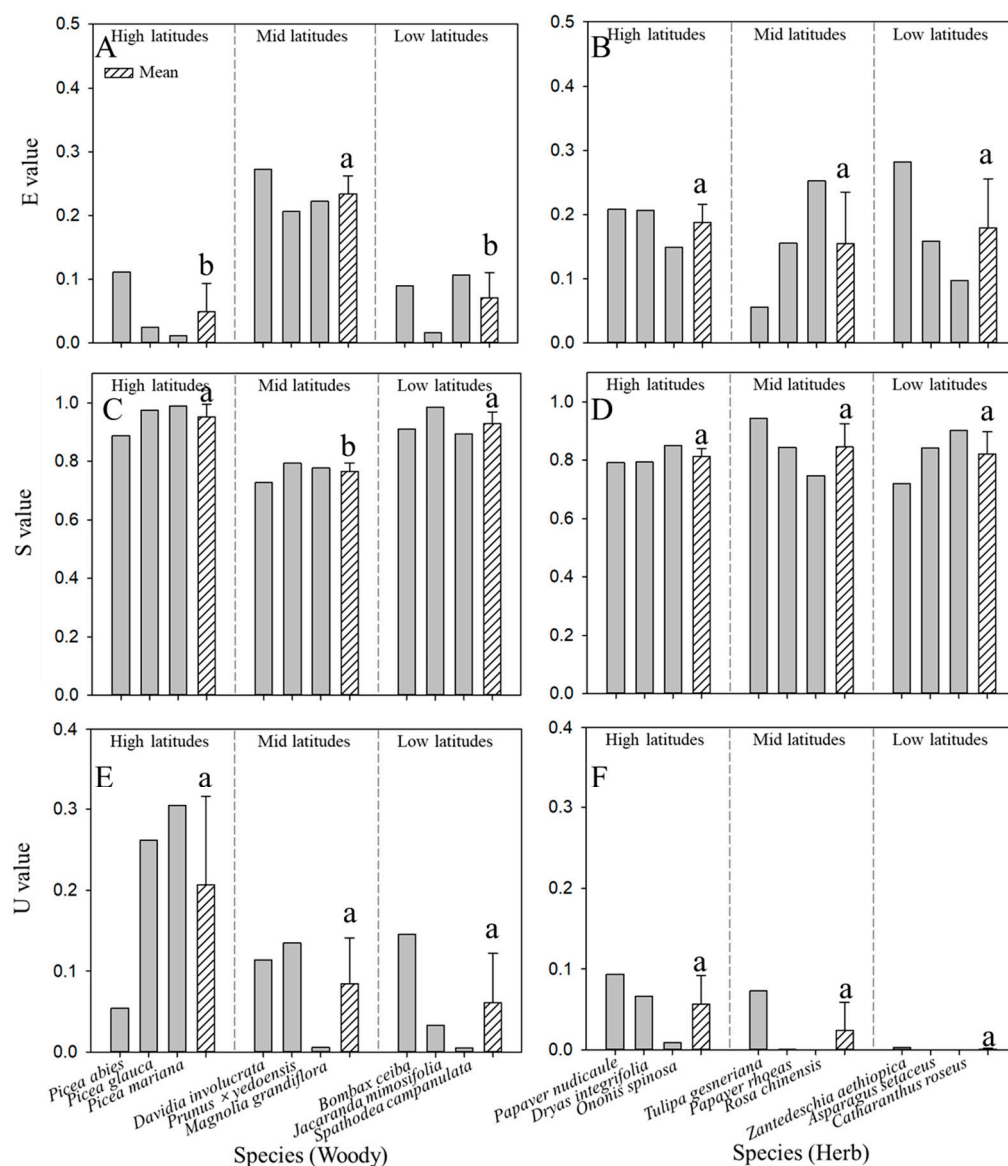


Figure 4. Niche dynamics of ornamental plants originating from different latitudes between introduced and native regions. E: niche expansions; S: niche stability; U: niche unfilling. The lower-case letters showed the significant difference ($p < 0.05$) between the mean of each value in woody and herbaceous ornamental plants at different latitudes. (A) E value of woody plants originating from different latitudes; (B) E value of herbaceous plants originating from different latitudes; (C) S value of woody plants originating from different latitudes; (D) S value of herbaceous plants originating from different latitudes; (E) U value of woody plants originating from different latitudes; (F) U value of herbaceous plants originating from different latitudes.

The niche breadth ratio (Br) values of the three woody plants from high latitudes were -0.062 , 0.279 , and 0.352 , while those of the three woody plants from mid-latitudes were all less than 0, at -0.198 , -0.086 , and -0.246 . For the three woody species from low latitudes, two had Br values greater than 0 (0.064 and 0.017), and one had a value less than 0 (-0.009) (Figure 5A). For herbaceous plants, the Br values of plants originating at different latitudes were all less than 0, except for *Tulipa gesneriana* originating in the mid-latitudes (Figure 5B). Both woody and herbaceous plants had Sim values greater than 0.5 (Figure 5C,D). Therefore, although mid-latitude woody plants did not show niche conservatism, herbaceous plants did not show niche conservatism at any latitudes based on Br values. However, when Br values were considered in combination with Sim values, all species at all latitudes showed niche conservatism (Figure 5).

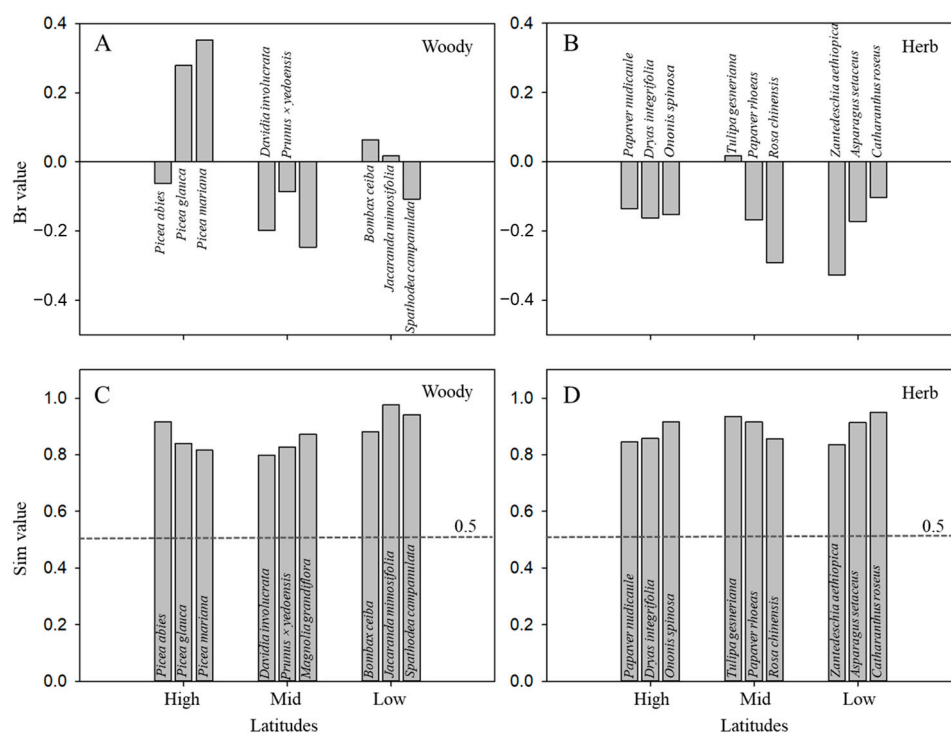


Figure 5. Niche conservatism analysis of ornamental plants originating from different latitudes between introduced and native regions. Br: breadth ratio; Sim: similarity index. (A) Br value of woody plants originating from different latitudes; (B) Br value of herbaceous plants originating from different latitudes; (C) Sim value of woody plants originating from different latitudes; (D) Sim value of herbaceous plants originating from different latitudes.

3.3. The Commonality of Factors Affecting the Distributions of Plants at Different Latitudes

Principal component analysis was performed for the importance values of the influencing factors affecting the distributions of woody and herbaceous plants in their native and invasive regions. Since many environmental factors affected each species, the cumulative contribution rates of the top two principal components for both woody and herbaceous plants were not very high, at 47.99% for woody plants (Figure 6A). In the case of herbaceous plants, the value was 37.37% (Figure 6B). In terms of the factors influencing the woody plants from different latitudes, the plants originating in the high latitudes were relatively conservative compared with those originating in the middle and low latitudes. However, the influence indexes in the middle and low latitudes were quite different, and the confidence ellipse was vertically distributed (Figure 6A). Among herbaceous plants, the plants with mid-latitude origins were conservative in their environmental adaptability and extended throughout by high and low latitudes, while the factors influencing plants originating from high and low latitudes were quite different, and the confidence ellipses of these groups of plants were also vertically distributed (Figure 6B).

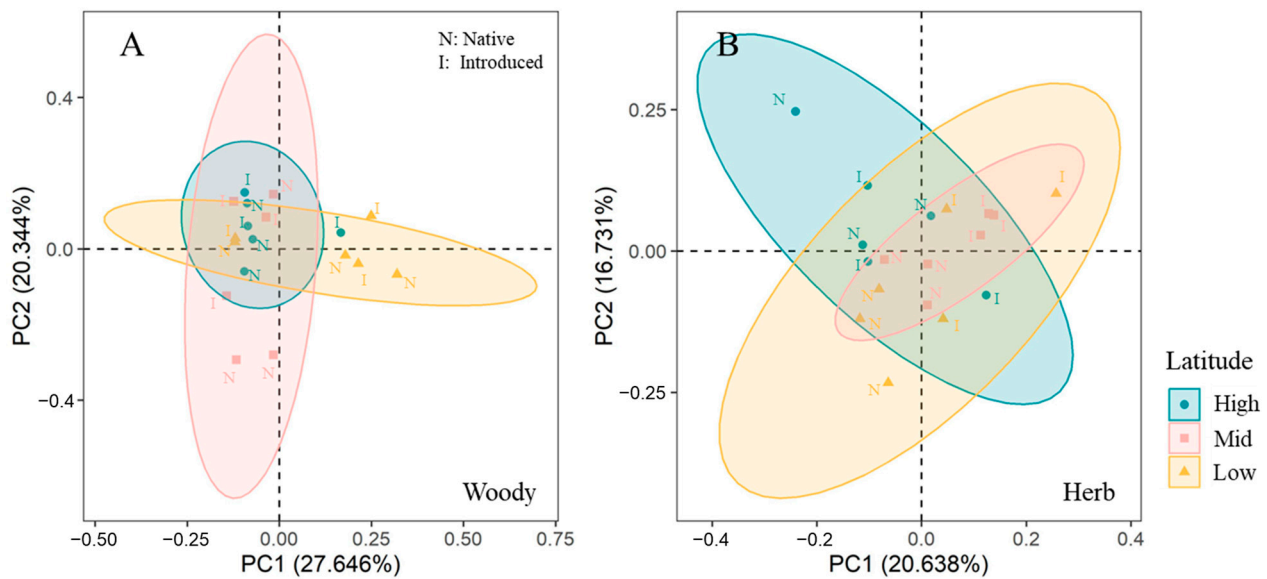


Figure 6. Principal component analysis of the importance values of influential factors affecting the distributions of woody and herbaceous plants in their native and invasive regions. (A) principal component analysis in woody plants; (B) principal component analysis in herbaceous plants.

4. Discussion

The extensive impact of biological invasion on the global scale has attracted increasing attention [31], and alien invasive plant species have serious impacts on the environment, ecosystem services and human health [32]. Researchers generally believe that the spatial distribution of invasive plants is mainly influenced by the biological characteristics of the invasive species, the natural environment, and human activities [33]. For plant dispersal, biological characteristics form the foundation, human activities provide opportunities, and natural environmental factors are the key to whether plants can successfully invade [34]. Cultivation, which relies almost entirely on human activities, undoubtedly provides many opportunities for plant proliferation and invasion. In recent years, the risk of plant invasion brought about by the global circulation of horticultural plants has attracted much attention [3], and researchers have also called for the establishment of a scientific control framework to address the risks caused by potential invasion of horticultural plants [35], especially in the context of global climate change [17]. On the other hand, plants originating from different environments have gradually evolved genetic characteristics through the process of adapting to the environment of their origin, reflecting their ability to adapt to new environments as invasive plants. Based on the reasoning outlined above, this study selected common ornamental plants originating from different latitudes and analyzed the factors driving their distributions in native and introduced areas, as well as shifts in ecological niches during the diffusion process, our aim was to understand the driving mechanisms of plants with different origins and their invasive capacity.

However, it must be noted that people often build facilities to provide artificial environments for horticultural plants so that they can be grown in places where the natural environment is not suitable, and the occurrence records of species that can be collected are difficult to distinguish whether has been affected by facilities or not. The resulting occurrence records affect species distribution models and ecological niche models built based on natural environmental factors. Therefore, this study divided the research subjects into herbaceous and woody species to discuss this bias (compared to herbaceous plants, large woody plants are more difficult to establish in artificial facilities). The results showed that the most important factors driving the distributions of all the plant species in this study were generally climatic factors (Figures 2 and 3). The distributions of plants originating at different latitudes are driven by different factors (Table S3). Plants from high-latitude

regions are mainly limited by temperature-related factors, while those from mid-latitude regions are influenced by precipitation-related factors, and those from low-latitude regions are influenced by temperature-related factors (Figures 2 and 3, and Table S3). When we ranked the three most influential factors affecting the distribution of each species, we found that the most important factor driving the distribution of ornamental plants in their introduced regions was urban land, and this was true for both herbaceous and woody plant species (Figure 3 and Table S3). This may be the ornamental plants are often cultivated for human needs, and their dispersal often occurs in human residential areas. In addition, due to the favorable conditions provided by people, urban land surpassed natural environmental factors as the primary factor driving plant distributions in introduced areas. This finding highlights the challenges associated with preventing and controlling the invasion risks of ornamental plants. As food crops, which are distributed globally, are rarely seen in the wild. The possible reason for this is that crops have been extensively managed during their introduction and long cultivation history, causing them to lose their competitiveness in the wild. However, many ornamental plants do not suffer from the effects of extensive management or the loss of natural dispersal ability such as food crops, which is a possible reason for the potential invasion risk posed by ornamental plants that has been widely studied and considered [15,31,36]. Therefore, further understanding the factors driving the dispersal and establishment of ornamental plants, especially in the absence of human interference, and exploring whether it is driven by active invasion or passive cultivation, is crucial for evaluating the invasion mechanisms of ornamental plants in the future.

The ecological niche plays an important role in understanding the mechanism of spatial and temporal distribution patterns of species [13]. It is assumed that the climatic niche requirements of invasive species are conservative between their native and invasive ranges, which is the key to predicting invasion risks based on species distribution models [15], but this assumption has been challenged by evidence of niche shifts in some species, including plant species [30,37]. However, a large-scale test of niche conservatism among 50 terrestrial invasive plant species between Eurasia, North America, and Australia showed that substantial niche shifts are rare among terrestrial plant invaders, providing support for the appropriate use of ecological niche models for the prediction of both biological invasions and responses to climate change [15]. Nevertheless, a large amount of research on plant invasion still focuses mainly on species that accidentally introduced, we know that human activities, especially cultivation activities, have brought about plant invasion, which has caused concern but has received less attention. To meet cultivation needs, humans not only provide migration opportunities and favorable conditions for plants to grow in new habitats but also, through various means, change some of the genetic characteristics of plants, enabling their adaptation to new environments. For example, wheat, as a major crop species worldwide, does not retain the niche space inherited from its wild ancestors, which indicates that cultivation may have a stronger impact on niche transfer than most plant invasions [14]. Compared with food crops, horticultural plants, especially those used for ornamental purposes, are not necessary for life. Therefore, people do not invest as much energy to breed or provide them with the optimum agronomic measures as they do for food crops. Hence, whether the niches of horticultural plants have shifted remains unclear.

Niche dynamics may directly affect the invasive ability of plant species. Although the niche of wheat has shifted, artificial measures have caused it to lose its individual competitiveness [14], weakening the possibility of its invasion of new habitats (wheat often relies heavily on artificially created agricultural ecosystems and its occurrence in the wild is negligible). Horticultural plants receive many migration opportunities and may retain the ability to survive in the wild, which may also be one of the reasons for concern expressed by many studies over the invasion risks of horticultural plants [31]. In this study, the niche dynamics and niche conservatism of herbaceous and woody ornamental plants originating from different latitudes were tested. The results showed that only the E value and S value in the niche dynamics of woody plants showed significant differences. The E value of plants with a mid-latitude origin was significantly higher than that of plants with high-

latitude and low-latitude origins, while the S value of plants with a mid-latitude origin was significantly lower than that of plants originating in the other two latitudes, indicating that woody plants of a mid-latitude origin had higher invasion potential (Figure 4). The results of the niche conservatism test showed that the breadth ratio (Br) values between introduced and native herbaceous plant species were <0 except for *Tulipa gesneriana*, indicating that the niche breadths of plants were much wider in the introduced ranges than in the native ranges (Figure 5). That is, the ecological niche was not conserved. However, among the woody species, except for plants originating from mid-latitudes with Br values less than 0, most plants had Br values greater than 0 (Figure 5). Therefore, according to the niche dynamics and conservatism tests, among the woody plants, those with mid-latitude origins showed stronger invasion characteristics. Although herbaceous plants also showed nonconservatism with respect to ecological niches, there was no difference between plants with different originating latitudes.

The differences between herbaceous and woody plants may be related to the influences of facilities with artificial environments. Herbaceous plants may be planted in courtyards, greenhouses and other facilities due to their small size, and these facilities can easily alter the growth environment, allowing the plants to grow in areas where the actual natural environment is not suitable. These occurrences may be mistaken as the result of natural invasion or ecological niche migration in models created based on natural environmental conditions. In this study, principal component analysis of the influence of environmental factors also showed that there was a large overlap of the environmental factors affecting herbaceous plants with different latitudinal origins (Figure 6). In this study, herbaceous and woody plants were analyzed separately to eliminate the interference described previously when analyzing the invasive ability of plants originating from different latitudes. The results also indicated that in the process of constructing an ensemble of ecological niche models, more attention should be given to those species that may be cultivated in artificial environments to prevent the illusion of ecological niche migration. On the other hand, we should also note that the niche similarity index (Sim) of all the species in the introduced range regardless of origin was higher than 0.8 (Figure 5), which is much higher than that of wheat and its wild counterparts, with Sim values of 0.57 and 0.18, respectively [14]. These results indicate that the ecological niche similarity of the introduced and native species of ornamental plants involved in this study is still high. They also support the rationale presented previously, that is, ornamental plants are subject to much less artificial selection pressure, and the ecological niche of a species in its introduction area does not shift a great deal.

5. Conclusions

The most important driving factors for the distribution of each species were climate-related factors in this study. Plants originating from high-latitude regions are mainly influenced by temperature-related features, while plants originating from mid-latitude regions are influenced by precipitation-related features, and plants originating from low-latitude regions are influenced by temperature-related features. However, for species in introduced areas, urban land became the most influential factor, which may also reflect the importance and driving force of human activities for the spread of ornamental plants. The results of the niche dynamics test showed that only woody plants originating in mid-latitude regions showed greater distributions and diffusion abilities than those originating in high and low latitudes. The niche breadth ratios showed that the niche widths of the herbaceous plants originating from different latitudes were generally larger than those in the native region, and only woody plants originating from mid latitudes showed similar results. However, the niche similarity of all ornamental plants between the introduced and native regions was still high, showing that all species in the introduced areas inherited niche characteristics from plants in their native regions. This study also pointed out that smaller herbaceous ornamental plants are more likely to be cultivated by humans in facilities, which leads to their geographical expansion to places where the natural environment is not

suitable for their growth. It also reminds us to be careful of the biases of human interference when using natural environmental factors to build an ensemble of ecological niche models and niche dynamic models.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15070877/s1>, Table S1: Plant species of different latitudinal origins; Table S2: The importance values of the variables determining the spatial distributions of all plants in native and introduced areas from different latitudes; Table S3: The chi-square test was used to analyze the significant difference in environmental factors and latitudes.

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