



Afforestation and climatic niche dynamics of black locust (*Robinia pseudoacacia*)



Guoqing Li^{a,b}, Xiaoqin Zhang^{b,c}, Jinghua Huang^{a,b}, Zhongming Wen^{a,b}, Sheng Du^{a,b,*}

^a State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Northwest A&F University, Yangling 712100, China

^b Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resources, Yangling 712100, China

^c College of Landscape Engineering, Heze University, Heze 274015, China

ARTICLE INFO

Keywords:

Black locust
Afforestation
Niche dynamics
Niche conservatism
Occurrence records

ABSTRACT

Many tree species have been introduced outside their native ranges, but there is little knowledge of their niche dynamics during afforestation in different regions. Here, we test the climatic niche dynamics of a species, black locust (*Robinia pseudoacacia*), planted worldwide, between its native range (southeastern parts of United States) and four introduced ranges (North America, Europe, East Asia, and Australia). A principal component analysis method with kernel smoothers was applied to species' occurrence densities to investigate the climatic niche centroid, breadth and unfilling/expansion between native and introduced ranges of black locust. The niche equivalency test, the niche similarity test, and the niche centroid/breadth shift tests were used to evaluate the conservatism and dynamics of realized niche of black locust. Niche equivalency/similarity tests show that only the European population has the same identical climatic niche as the native population and all introduced population in four areas are similar to native population than expected by chance with niche overlap between native and introduced areas ranging from 0.13 to 0.4. Niche centroid/breadth shift tests reveal that the niche centroid of black locust will significantly shift to warm or colder areas, as well as drier areas, and the niche breadth of black locust will significantly broaden both in water and heat gradients in the four introduced ranges separately. Niche partitioning shows that the proportion of niche unfilling occurred from 0 to 27% and that of niche expansion occurred in the 42–83% range. Our results imply that the internal causes of realized niche dynamics of black locust are mainly due to the release of biotic constraints and change in dispersal capability, but the relative importance of these factors is different among the four introduced ranges. Our study suggests that black locust conserves its climatic niche in the afforestation process allowing future studies to use ecological niche models to predict areas with suitable habitat for introduction and cultivation around the world and respond to climate change needs.

1. Introduction

Ecological niche models (ENMs) have been widely used to estimate the realized niches and predict the potential distribution of species for conservation, invasion, and afforestation purposes (Peterson et al., 2011; Booth et al., 2014). The key assumption of ENMs is that species tend to grow and develop under similar climatic conditions in native and introduced or invasive ranges across space and time, which is named as niche conservatism assumption. Soberon and Nakamura (2009) suggest that conservatism in a strict sense should refer to the fundamental niche. However, as we often do not know the shape of the fundamental niche, so the niche conservation concept has been widely tested using invaded areas. Petitpierre et al. (2012) reported a large-scale test of climatic niche conservatism for 50 invasive plant species

from Eurasia, North America, and Australia and demonstrated that niche shifts are rare in invasive plant species. Nevertheless, this assumption has been challenged for some invasive species when introduced in new regions (Early and Sax, 2014; Kumar et al., 2015; Tingley et al., 2015). The mechanism underlying the difference may be: (1) rapid adaptive evolution of the species' fundamental niches due to high standing genetic variation and recombination, and (2) changes in the realized niches following the release from biotic constraints on native distributions such as predators, pathogens, or competitors, without any adaptive change to the fundamental climatic niche.

Recent discussions regarding realized niche changes are mainly focused on invasive species (Guisan et al., 2014; Tingley et al., 2015). Evaluation of niche dynamics of tree species for afforestation is not yet a common goal in ecological and forestry studies (Vetaas, 2002). In

* Corresponding author at: Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resources, Yangling, Shaanxi 712100, China.
E-mail address: shengdu@ms.iswc.ac.cn (S. Du).

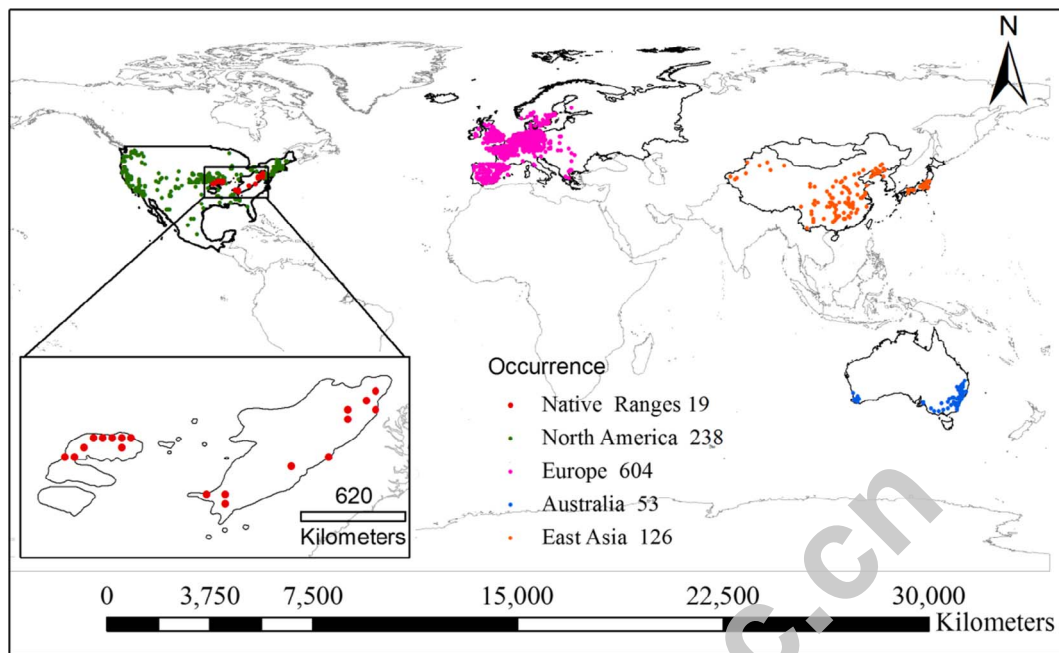


Fig. 1. Spatial distribution of global occurrences of black locust (*Robinia pseudoacacia*) in its native ranges and four introduced ranges (black polygons, North America, Europe, Eastern Asia, and Australia).

general, invasive species and tree species for afforestation expand from their native ranges in similar ways, for instance, through birds and human activities; however, their ecological consequences tend to be different. Invasive species may transform as a threat by invading the ecosystem in non-native regions (Richardson and Rejmanek, 2011), whereas afforestation species may accelerate the restoration of introduced ecosystem in non-native regions (Wang, 2006; Boothroyd-Roberts et al., 2013). At present, the introduction of trees to other regions is based on the concept of Hutchinson's realized and fundamental niches (Booth et al., 1988; Soberon and Nakamura, 2009). Booth et al. (1988) showed for the first time how information from native and introduced ranges could be used to provide some indication of the fundamental niche of tree species. However, whether the realized niche in the introduced ranges is shifting due to biological or movement factors remains unknown for many tree species. Thus, exploring the realized niche dynamics of tree species during its afforestation is a critical need for cross-regional tree introduction and cultivation for afforestation purposes at a global scale.

ENMs have been used to explore niche dynamics for some time, but statistically quantifying similarities or differences between two species or ranges has lagged in comparison (Glennon et al., 2014). Currently, the two most frequently used statistical tests that quantify niche dynamics and test hypotheses of niche divergence or conservatism are the niche similarity test and the niche equivalency test. These tests could indicate whether niches are different between species or ranges, but they cannot inform how niches differ between species or ranges. A recent ordination method (Broennimann et al., 2012) can visualize the niche dimensions and inform how optimal or different niches are, and their breadth in environmental space between species or ranges. Based on this method, Dellinger et al. (2016) proposed an explicit test for niche centroid shift and niche broadening or contraction in an environmental niche space. Combining these methods could provide an excellent framework to gain insights on species' realized niche change patterns and infer biological processes underlying species niche development between species or ranges.

Black locust (*Robinia pseudoacacia*) is a tree native to North America (southeastern parts of United States) (Little, 1976) that has been widely planted around the world for a long time (Cierjacks et al., 2013). Data from the Global Biodiversity Information Facility (GBIF, 2015) and

Chinese Virtual Herbarium (CVH, 2015) databases show that black locust has naturalized in approximately 35 countries, spanning North America, Europe, East Asia, and Australia. Li et al. (2014a) used maximum entropy modelling to identify areas around the world which experience similar climatic conditions. However, its climatic niche dynamics have not been tested across the different continental regions (e.g., North America, Europe, East Asia, and Australia). Land managers urgently need such information for managing current afforestation and planning future afforestation activities. To achieve these goals, we used a framework established by Broennimann et al. (2012) to visualize the realized niche change patterns of black locust and a series of significant tests (for details see Methods section) to test its niche divergence or conservatism across the four regions *vis-a-vis* its native region. Our study mainly focuses on answering the following questions: Did the climatic niche change for black locust during its afforestation around the world? What can we learn from the observed patterns of niche dynamics of black locust across the four introduced ranges? The data obtained from this study will augment the theoretical basis for the successful introduction and cultivation of black locust worldwide.

2. Materials and methods

2.1. Species occurrence data

Occurrence records of black locust were collected from the herbarium data in Global Biodiversity Information Facility database (GBIF) and the Chinese Virtual Herbarium database (CVH). A total of 32,674 specimens (32,434 from GBIF and 240 from CVH) were identified with coordinates. We plotted all 32,674 records on the world map with a $0.5^\circ \times 0.5^\circ$ spatial resolution, such that the world map was divided into grid cells (land area with 584,521 cells) with 300 rows and 720 columns. If a grid cell contains one or more specimens, we would assume that the grid was suitable for black locust survival. Then, a binary grid map (presence/absence map) with a $0.5^\circ \times 0.5^\circ$ spatial resolution was converted into points by using the "raster-to-point" function in ArcGIS 9.3. Finally, we got a total of 1174 occurrence points of black locust. The detailed coordinates of each occurrence point have been provided by Li et al. (2014a). To meet the requirements of our study, we categorized the occurrence records into six groups: native range records

(19), North American range records (238), European range records (604), East Asian range records (126), Australian range records (53), and others (134). For this study, we focused on the native region and four introduced or cultivated regions (North America, Europe, East Asia, and Australia) (Fig. 1).

2.2. Climatic variables

We used 13 climatic factors to characterize the climatic niche of black locust around the world (raster layers with resolution of $0.5^\circ \times 0.5^\circ$). These included annual mean temperature (AMT), maximum temperature of the warmest month (MTWM), minimum temperature of the coldest month (MTCM), annual range of temperature ($ART = MTWM - MTCM$), annual precipitation (AP), precipitation of the wettest month (PWM), precipitation of the driest month (PDM), precipitation of seasonality ($PSD = \text{Monthly coefficient of variation of precipitation}$), annual biotemperature ($ABT = \sum_{i=1}^{12} T_i/12$, T is $0^\circ\text{C} < T < 30^\circ\text{C}$ mean monthly temperature), warmth index ($WI = \sum_{i=1}^{12} (T_i - 5)$, T is $> 5^\circ\text{C}$ mean monthly temperature), coldness index ($CI = \sum_{i=1}^{12} (T_i - 5)$, T is $< 5^\circ\text{C}$ mean monthly temperature), potential evapotranspiration rate ($PER = 58.93 \times ABT/AP$), and humidity index ($HI = AP/WI$). These 13 variables have been successfully applied to the prediction of global suitable habitat for black locust (Li et al., 2014a) and oriental arborvitae (*Platycladus orientalis*, Li et al., 2016). Information regarding all the basic climatic layers was obtained from the online WorldClim database (Hijmans et al., 2005; Worldclim, 2015).

2.3. Calculating niche overlap and statistically comparing niche dynamics

2.3.1. Calculating niche overlap and niche dynamics

We used the principal component analysis (PCA) approach proposed by Broennimann et al. (2012), which allows description of the environmental space occupied by a species based on its occurrence records without projecting data in the geographical space. In this method, species records are plotted on a gridded environmental space with 100×100 dimension and a kernel smoothing method is used to calculate the density of species occurrences. Niche overlap is calculated using a well-established Schoener's D metric that ranges from 0 (no overlap) to 1 (complete overlap). An unbiased estimate of D is calculated using a kernel density function that is applied to occurrence densities. Finally, species occurrence densities in environmental niche space are mapped using a principal component analysis (PCA).

Direct overlays of the calculated native and introduced occurrence densities in the two-dimensional PCA space can be used to visualize the dynamics of niche centroid and breadth of the two dimensions between native and introduced ranges. They can also provide quantitative indication concerning the niche filling and expansion. Following Petitpierre et al. (2012), three categories of niches are calculated as follows: niche stability—the proportion of the densities in the introduced niche that overlap with native niche; niche unfilling—the proportion of the densities in the native niche that do not overlap with the occupied introduced niche; and niche expansion—the proportion of the densities in the introduced niche that do not overlap with the occupied native niche (or 1-stability). The niche partitioning analysis is performed on the union environment of native and invaded ranges rather than the intersection environment of native and invaded ranges.

2.3.2. Statistical test of niche dynamics

Statistical analysis of niche dynamics was carried out using two statistical tests: niche similarity test and niche equivalency test. The niche similarity test determines if the realized niche of the native range is better at predicting the realized niche of introduced ranges than randomly generated niches from a background region (Broennimann et al., 2012). This procedure is repeated 100 times to generate a null

distribution of D metric to determine statistical significance. If the observed D is less than the null distribution, it indicates realized niche divergence and values greater than the null indicate that realized niches are more similar than random.

The niche equivalency test directly compares the realized niches of native and introduced ranges to determine how identical the two realized niches are to each other (Broennimann et al., 2012). In this method, the occurrences of the two groups in question are randomly reassigned into two data sets to recalculate the D values. This procedure is repeated 100 times to generate a null distribution of D metric to determine statistical significance. If the observed D falls above the null distribution indicated, then the hypothesis of realized niche equivalency is accepted and the realized niches are considered equivalent. This is a strict test for realized niche conservatism and therefore, non-significant results only indicate that realized niches are not identical, but not that the realized niches are dissimilar.

2.3.3. Statistical test of shift in optimal niche position and niche breadth

The significant changes in optimal niche position and niche breadth of black locust between native and introduced populations is tested using the method developed by Dellinger et al. (2016), which is an expansion of the PCA approach proposed by Broennimann et al. (2012). We re-sampled occurrence records 100 times with replacement in either of the ranges and recalculated PCAs each time. For each separate PCA axis, the niche centroid was represented as the median of these values, and the niche breadth as the distance between the 0.025 and 0.975 quantiles. We calculated the differences in niche centroid in each bootstrap run between introduced and native ranges. A significant shift in niche centroid is implied if the central 95% of the calculated differences does not include zero. We also calculated the niche breadth rate in each bootstrap run between introduced and native ranges. The niche breadth was considered to be significantly smaller or broader in the introduced range if the central 95% of the calculated introduced/native range ratios was < 1 or > 1 , respectively.

3. Results

3.1. Climatic niche overlap visualization

Climatic niche overlap analysis was carried out in a gridded climatic space formed by the first two axes of principal component analysis based on 13 climatic variables. These first two axes accounted for 71.42% of the variation in the data (axis 1: 46.1%; axis 2: 25.32%; supplementary materials Fig. S1). The first PCA axis is dominated by the heat gradient, whereas the second axis predominantly represents the water gradient. Climatic niche overlap was visualized as shown in Fig. 2, which reveals climatic niche overlap between native and European population is the highest ($D = 0.40$), whereas niche overlap between native and East Asian population is the lowest ($D = 0.13$) (Table 1, Fig. 2).

3.2. Climatic niche equivalency and similarity tests

Niche equivalency tests showed that only the European population had the same identical climatic niche as the native population (100 permutations test $P < .05$, indicating that their niches are equivalent), but the East Asian, Australian, and North American populations did not show identical climatic niches as native population (100 permutations test $P > .05$, Fig. 3, indicating that their niches are not equivalent). Niche similarity tests showed that all populations introduced in four areas (North American, European, Australian, and East Asian) were more similar to the native population than expected by chance (100 permutations test $P < .05$; Fig. 4, indicating that their niches are similarity).

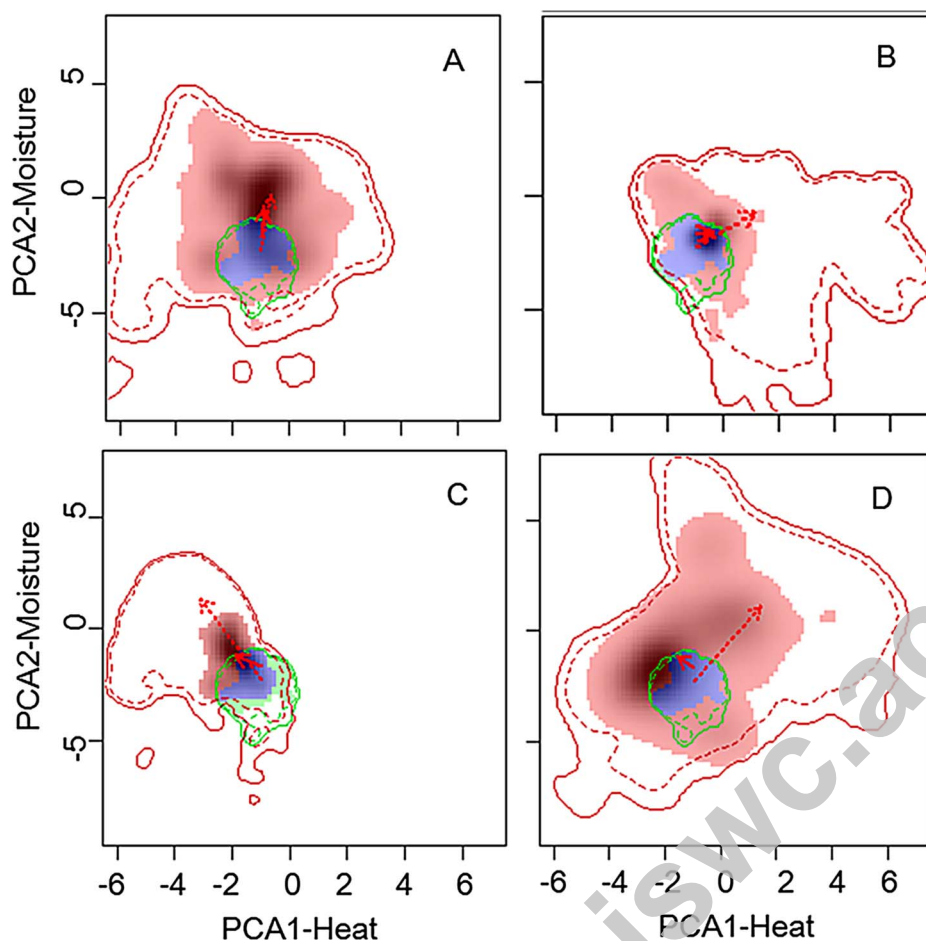


Fig. 2. Niche overlaps and dynamics of black locust (*Robinia pseudoacacia*) between introduced and native areas in climatic space. (A) North America; (B) Europe; (C) Australia; (D) East Asia. Solid and dashed lines represent 100% and 75% of the available environment in native range (green lines) and introduced range (red lines). Green areas represent climates only occupied in the native range, blue indicates climates occupied in both the native and introduced range. Shading indicates the density of occurrences of black locust by cell in the introduced range. The red arrows show how the centroid of the climatic niche (solid) and background extent (dotted) has moved between two ranges. The first PCA axis is mainly determined by heat gradient (high to low, 46.1%), the second axis chiefly represent water gradient (wet to dry, 25.32%). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Niche overlap value and the proportion of niche change of black locust (*Robinia pseudoacacia*) between native and introduced ranges.

Region	Niche overlap	Niche stability	Niche unfilling	Niche expansion
North America-Native	0.24	0.27	0.00	0.78
Europe-Native	0.40	0.58	0.02	0.42
Australia-Native	0.28	0.38	0.27	0.62
East Asia-Native	0.13	0.17	0.00	0.83

3.3. Climatic niche stability, expansion, and unfilling

Climatic niche partitioning showed that the proportion of 17–58% of the four introduced populations' climatic niches is stability niche values and the proportion of 42–83% of their climatic niche is expansion niche (novel habitat; Table 1; Fig. 2). There are no or very few unfilling climatic niches in the North American, European, and East Asian populations (0–2%), whereas there are large unfilling climatic niches in the Australian population (27%, Table 1).

Niche centroid shift tests showed that the climatic niche centroid of four introduced populations would significantly change from left to right (more and more cold) or right to left (increasingly warm) along the first PCA axis ($p < .05$), whereas it would significantly change from bottom to top (increasingly dry) along the second PCA axis ($p < .05$), except for the European population ($p > .05$) (Table 2). It indicates that the realized climatic niche of black locust has the potential to colonize and adapt to areas far colder or warmer, as well as drier than its native range.

Niche breadth shift tests showed that all four introduced

populations have significantly broadened their climatic niche breadth along the two PCA axes, except for the Australian population along the first PCA axis (Table 2). The largest climatic niche breadth broadening is seen in the Asian population (2.71 times more than that of the native population along the first PCA axis, 4.40 times more than that of the native population along the second PCA axis), whereas the Australian population had the least (not broad along the first PCA axis, 1.70 times more than that of the native population along the second PCA axis).

4. Discussion

The process of introduction of tree species around the world is generally based on niche concept and the principle of climatic niche similarity (Booth et al., 1988; Booth, 2016). According to the BAM (biotic, abiotic, and movements) framework to explain niche and distribution (Soberon and Nakamura, 2009), the information of species interaction and species dispersal capability have been included in occurrence data. Thus, the first niche model applied when considering introductions outside the native distribution is usually based on the species' estimated realized niche, not the fundamental niche. In this study, using black locust as an example, our results demonstrate that European population shows that realized niche of European population is not only similar to, but also identical to the native population. European population shows very strict realized niche conservatism. It indicates that European population has the same biological processes governing distribution of black locust as in native range, such as predators, pathogens, or competitors. North America, East Asian and Australian populations show that realized niche is only similar but not identical to that of the native population. It suggests that the niche of black locust is also conserved in North America, East Asian and

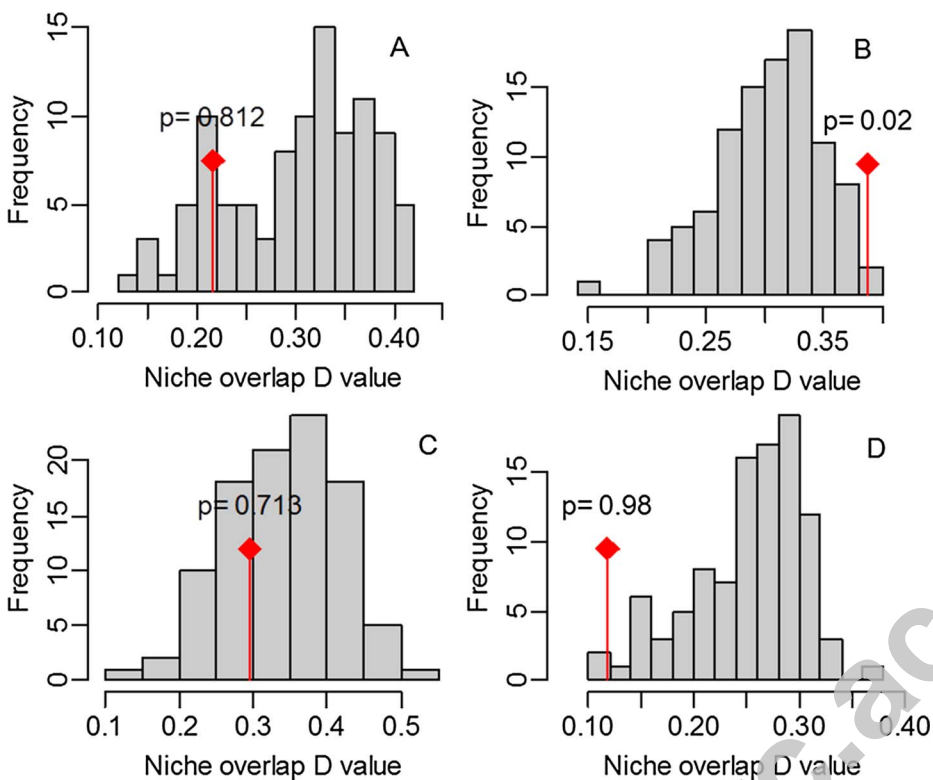


Fig. 3. Niche equivalency test of black locust (*Robinia pseudoacacia*) with 100 replication between native and four introduced ranges. (A) North America; (B) Europe; (C) Australia; (D) East Asia. Bars represent the frequency of niche overlap D value. Red line represents observed niche overlap D value. p represents p value of the significant test.

Australian ranges. Niche conservatism of black locust in the four introduced ranges indicates that we can estimate much of the suitable habitat of black locust using only native distribution data when we lack data from introductions outside, which is just as Booth's (2016) work of Centre for Agriculture and Biosciences International (CABI) Forestry Compendium's (<http://www.cabi.org/fc/>) work on analyses of tree

climatic requirements.

Niche partitioning data reveals that black locust have successfully expanded 42–83% of their realized climatic niche when introduced outside their native area. This may be due to unlimited dispersal capability and lack of natural enemies during its establishment in its fundamental climatic niche and geographical space according to the BAM

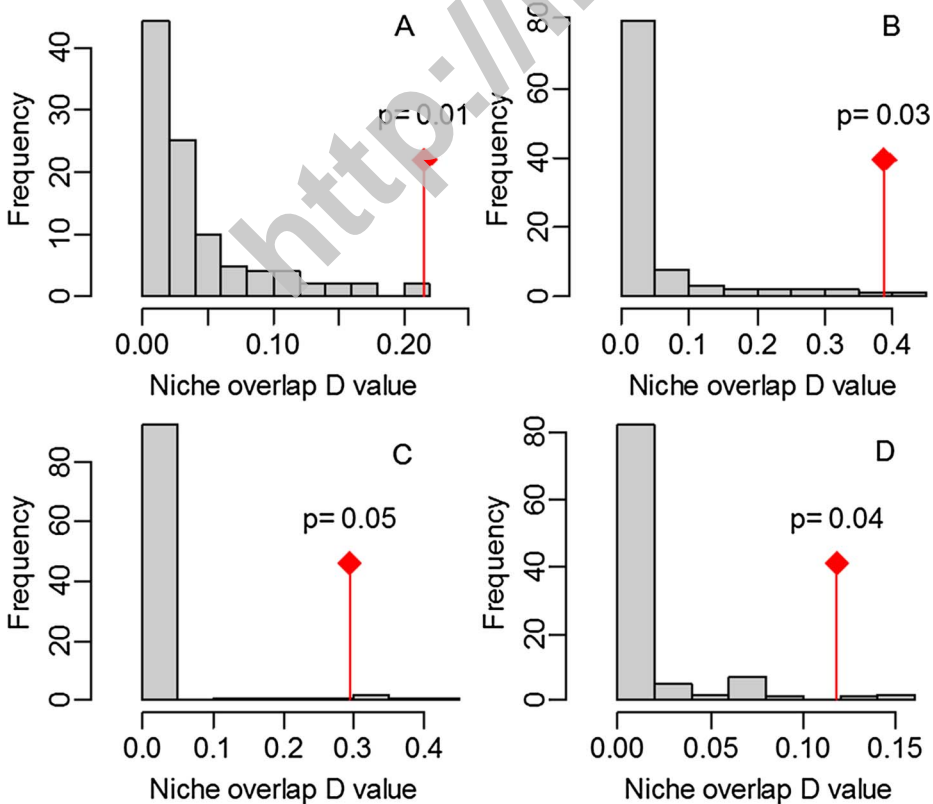


Fig. 4. Niche similarity test of black locust (*Robinia pseudoacacia*) with 100 replication between native and four introduced ranges. (A) North America; (B) Europe; (C) Australia; (D) East Asia. Bars represent the frequency of niche overlap D value. Red lines represent observed niche overlap D value. p represents p value of the significant test.

Table 2
Results of niche centroid/breadth shift test of black locust (*Robinia pseudoacacia*).

Region	Niche centroid shift test		Niche breadth shift test	
	PC1	PC2	PC1	PC2
North America-Native	0.12C	1.22D	2.13B	2.80B
	0.04,0.24	0.88,1.76	1.90,3.52	2.35,3.31
Europe-Native	0.60C	0.06 ns	1.39B	2.17B
	0.54,0.70	-0.22,0.37	1.27,2.29	1.99,2.65
Australia-Native	-0.91 W	0.47D	1.02 ns	1.70B
	-0.98, -0.67	0.08,1.04	0.86,1.71	1.38,2.03
East Asia-Native	-0.57 W	0.55D	2.71B	4.40B
	-0.73, -0.13	0.12,0.99	2.41,4.52	3.13,5.18

Note: Change in niche centroids are classified as significant shift to colder area C, to warmer area W and to dryer area D or no significant ns to null distribution (Bold fonts). Changes in niche breadth are summarized as significant broadening B or no significant ns to null distribution (Bold fonts).

framework (Soberon and Nakamura, 2009). Li et al. (2014b) found that niche expansion in amphibians and reptiles often occurred in the early stages of introduction in a new region. Considering this point of view, it is likely that black locust may have been first introduced in Europe (1636), followed by parts of Australia (unknown), North America (unknown), and finally in East Asia (1860). Ancillotto et al. (2016) found evidence for niche expansion of Alexandrine parakeets (*Psittacula eupatria*) in the niche conservative situation. As such, they have 65–67% of their invasive distribution outside their native climatic niche, including colonization of areas far colder than their native range. They explained that interspecific facilitation with *P. krameri* may contribute to niche expansion and invasion success of *P. eupatria*. Prior to this, Strubbe et al. (2015) suggested that parakeet invasions into colder climates may be explained by prior-adaption to human modified habitats in the native range. Our study also shows similar and significant climatic niche expansion of black locust into colder or warmer areas, as well as dryer areas than its native range. Our results support the viewpoint of Strubbe et al. (2015) rather than Ancillotto et al. (2016), because black locust has been widely used as ornamental tree in human modified habitat at global scale (Li et al., 2014a) and the tree is strongly invasive and has been able to compete with other species outside of its native range (Cierjacks et al., 2013; Vitkova et al., 2017).

Besides, we have noticed that niche centroid shift direction of black locust is not the same as or even vertical to that of background climate condition (Fig. 2), which indicate that non-climatic factors are driving niche changes. We infer that the novel climatic niche of black locust in introduced areas may be due to the inclusion of sink population in occurrence records that have been used in the analysis. Unlimited dispersal can create source-sink dynamics in which immigration maintains species in habitats outside of their niches (Holt, 2009). Sink populations of tree species are more common than invasive species because reduction in the sink populations is unlikely because once tree species has been planted, it is extremely difficult to eliminate. For example, tree species is planted in sink habitat for special ecological purpose by local government, e.g. erosion control. These sink population will be protected and intervened by human for sustainable development, e.g. replanting seedlings or irrigation. So, sink records are likely included in our occurrence dataset, which would affect the analysis of niche dynamics, especially niche expansion. Sink population of black locust can survive but cannot reproduce in the sink habitat; thus, it is an unstable population in nature. Early and Sax (2014) observed instances that time since introduction decreased niche expansion for European plants introduced to North America, which is most likely related to sink records have been included in occurrence datasets. Therefore, the future climatic niche of black locust may decrease over time due to reduction in the sink population and loss of sink habitat when sustainable afforestation of black locust is prevented, especially in East Asia region.

Meanwhile, very few unfilling niche of black locust are observed in

the Europe, North America, and East Asia ranges, which is mostly due to prolonged and intensive afforestation programs that use black locust in these regions, where the ecological and economic value of black locust have been promoted and broadly recognized. On the contrary, there is the proportional of 27% unfilling niche in Australia, it indicates that black locust may be only a recent introduction or restrictions in some suitable place given its invasive nature (Richardson and Rejmanek, 2011). Strubbe et al. (2013, 2015) suggest that reduced propagule pressure can help a population contract its geographical range and environmental niche by environmental and demographic stochasticity and Allee effects. Such a process may occur in Australia, because the release of competition factors is conducive to reducing propagule pressure. Once it occurs, it indicates that the planted black locust in Australia may present discontinuous patches distribution pattern and the human management effect is less than the Allee effect.

Although we found evidences of niche conservatism of black locust, the niche expansion component had occurred, the climatic centroids had shifted, and the climatic niche breadths had broadened in four introduced ranges, which indicate some niche change in four introduced ranges. Many studies have confirmed the importance of pooling native and introduced/invasive occurrence records in estimate the niche of species whether its climatic niche is conservative or has shifted (e.g. Bodin et al., 1988; Broennimann and Guisan, 2008; Ancillotto et al., 2016), but most of these studies are ignoring the regional differences in introduced/invasive ranges. This research is to evaluate niche dynamics of the same species at different introduced ranges and demonstrate a complex pattern of realized niche dynamics across four continental regions, including North America, Europe, East Asia, and Australia. Therefore, we infer that ENMs train in the native records will fail to account for newly expanded climates in introduction range. Pooling both native and introduced records in the training process, the fitted climatic niche may imply an expanded or shifted part of fundamental niche in the introduced range due to release of competition. Because of regional differences in the release intensity of competition, different pooling strategies of native and introduced records may improve the niche and distribution estimation of black locust in different continental region. Such an inference needs to be further tested.

The climatic niche we study is mainly the realized niche of black locust and the internal causes of niche dynamics we discuss is based on the assumption of fundamental niche unchanged. Actually, whether the fundamental climatic niche of black locust could evolve over time remains unknown to date. Ecological studies have found support for niche conservatism in subspecies of a parakeet in different continents (Strubbe et al., 2015) and among a subspecies of Mexican birds (Peterson and Holt, 2003). Rodrigues et al. (2016) found that niche conservatism is not expressed at the subspecies level of *Trachemys dorbigni*, but it occurs during the invasion process. The controversy over species niche evolution is still evident in the literature and suggests the need for a series of physiological and ecological experiments, and complemented by mechanistic models to solve the longstanding mystery of niche evolution of black locust around the world. Besides, our evidences of niche conservatism are mainly depended on the niche similarity test, which is first used by Warren et al. (2008) and modified by Broennimann et al. (2012) in their kernel smoothers framework. Currently, this method has been challenged by Glennon et al. (2014) because it cannot distinguish the variance of niche breadth and background heterogeneity, which makes this style of niche similarity test give a misleading conclusion in some cases. Therefore, a further theoretical study should be implemented to confirm the degree of uncertainty of niche similarity test.

5. Conclusions

We conclude that niche conservatism occurs in black locust during its afforestation in four continental regions and supports the hypothesis of niche conservatism. Due to the long history of introduction and

release of competitiveness, black locust has expanded its habitat to warmer or colder areas, as well as drier areas and the niche breadth will broaden along with both water and heat gradients. When naturalized in local areas, the future climatic niche may decrease over time due to reduction in the sink population and loss of sink habitat unless replaced through sustainable afforestation of black locust, especially in East Asia. Besides, black locust conserves its native climatic niche in the afforestation process allowing future studies to use ecological niche models to predict areas with suitable habitat for introduction and cultivation around the world and respond to climate change needs.

Acknowledgements

The authors acknowledge two anonymous reviewers for their constructive comments, which significantly improved the manuscript. The project was supported financially by the National Key Research and Development Program of China (2017YFC0504601), the National Nature Science Foundation of China (No. 31300407, 31500449) and Key Cultivation Project of Chinese Academy of Sciences “The promotion and management of ecosystem functions of restored vegetation in Loess Plateau, China”.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.10.019>.

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