



NICHE AND INTERSPECIFIC ASSOCIATION OF DOMINANT TREE POPULATIONS OF *ZELKOVA SCHNEIDERIANA* COMMUNITIES IN EASTERN CHINA

NICHO Y ASOCIACIÓN INTERESPECÍFICA DE LAS POBLACIONES DE ÁRBOLES DOMINANTES DE LAS COMUNIDADES DE *ZELKOVA SCHNEIDERIANA* EN EL ESTE DE CHINA

Li-YUAN SHAO, GUANG-FU ZHANG*

Jiangsu Key Laboratory of Biodiversity and Biotechnology, School of Life Sciences, Nanjing Normal University, Nanjing, China

*Corresponding author: zhangguangfu@njnu.edu.cn

Abstract

Background: *Zelkova schneideriana* Hand.-Mazz., is an endangered species mainly distributed in subtropical China. Currently, little is known about its niche and interspecific association.

Questions: What are the niche characteristics of *Z. schneideriana* and other associated species? What are the interspecific associations between these species?

Study sites and dates: *Z. schneideriana* communities in Jiangsu, China in 2019.

Methods: Twenty-one 400 m² plots were studied for importance value, niche breadth and overlap, interspecific association of *Z. schneideriana* communities.

Results: In 39 species of tree layer, *Z. schneideriana* had the greatest importance value and niche breadth. For the first 10 dominant species, a considerable difference was detected by the Levins index (1.75 - 19.84) and Shannon-Wiener index (0.77 - 3.02). Forty-four out of the 45 species pairs had the value of niche similarity indices ≤ 0.5 ; 38 species pairs had the value of niche overlap indices ≤ 0.5 . Overall interspecific association was not a significantly negative association for variance ratio < 1 . χ^2 test and Spearman's correlation coefficient further revealed that above 60 % of species pairs had negative associations, suggesting most dominant species were slightly associated with other species or even independent.

Conclusions: *Z. schneideriana* was a constructive species. Dissimilarity in environmental requirements was found among most dominant tree species, thus decreasing competition. This is likely due to the unstable community in the early stage of succession.

Keywords: Importance value, Interspecific association, Niche breadth, Niche overlap, *Zelkova schneideriana*

Resumen

Antecedentes: *Zelkova schneideriana* Hand.-Mazz. es una especie en peligro de extinción con distribución en China subtropical. Actualmente, se conoce poco sobre su nicho y asociación interespecífica.

Preguntas: ¿Cuáles son las características de nicho de *Z. schneideriana* y especies asociadas? ¿Cuáles son las asociaciones interespecíficas?

Sitio de estudio y fechas: Sur de Jiangsu, China en 2019.

Métodos: Se estudiaron 21 parcelas de 400 m² en cuanto a valor de importancia, amplitud y superposición de nicho y asociación interespecífica de *Z. schneideriana*.

Resultados: De 39 especies del estrato arbóreo, *Z. schneideriana* tuvo el mayor valor de importancia y amplitud de nicho. Para las primeras 10 especies dominantes se detectó una diferencia considerable mediante los índices de Levins (1.75-19.84) y de Shannon-Wiener (0.77-3.02). Cuarenta y cuatro de los 45 pares de especies tuvieron un valor de índice de similitud de nicho ≤ 0.5 ; 38 pares presentaron índice de superposición de nichos ≤ 0.5 . La asociación interespecífica de estas especies no fue significativamente negativa para la relación de varianza < 1 . La prueba de ji-cuadrada y el coeficiente de correlación de Spearman revelaron asociación negativa para más del 60 % de los pares de especies, sugiriendo que la mayoría de las especies dominantes se asociaron ligeramente con otras especies o incluso fueron independientes.

Conclusión: *Z. schneideriana* fue una especie constructiva en las comunidades. Se encontró diferencia en los requisitos ambientales entre las especies dominantes, lo que disminuyó la competencia. Es probable que esto se deba a la inestabilidad en las primeras etapas de la sucesión.

Palabras clave: Amplitud de nicho, asociación interespecífica, superposición de nicho, valor de importancia.

As a rare and endangered tree species endemic to China, *Zelkova schneideriana* Hand.-Mazz. is a versatile material (Wu & Raven 2003, Yin 2013). Firstly, it can be used as a precious high-density wood timber (Jin et al. 2009). Secondly, its bark contains 46 % fiber, so it can be used to make artificial cotton, cord, and paper. Thirdly, it is an ornamental tree species, with a graceful crown, straight trunk, and red leaves in autumn. In addition, its leaves and bark are of great importance in Chinese Traditional Medicine. Unfortunately, over the past several decades, the distribution of its natural populations has significantly decreased due to deforestation and overharvest (Ma & Zhang 2009). Since 1999, *Z. schneideriana* has been listed as a national second-grade protected endangered plant species in China (Yin 2013).

According to the Flora of China Vol. 5, *Z. schneideriana* is distributed in 16 provinces in China (Wu & Raven 2003), with it primarily being distributed in subtropical regions of China (Ma & Zhang 2009). More recently, according to the results of the second key protected wild plant resources survey conducted in China, the mountainous area of southern Jiangsu is an area with a concentrated distribution of *Z. schneideriana* (Jiangsu Forestry Bureau 2017). Previous studies have focused on leaf architecture (Wang et al. 2001), phylogeny (Denk & Grimm 2015), genetic diversity (Liu et al. 2016), and seedling ecology (Yu et al. 2015); however, little is known about its niche and interspecific association.

A niche is the position of one species in a community in relation to other species. In other words, it refers to the spatial and temporal position and functional relationship of each species in the community (Grinnell 1917, Bai & Zhang 2017, Lu et al. 2020). Niche breadth can be used to reflect the utilization of resources, the distribution and quantity of species; niche overlap can be measured to determine the degree of similarity between species in their ability to exploit resources or adapt to the environment (Colwell & Futuyma 1971). Thus, a niche may reflect the position, function, and importance of a species in a community. Interspecific association refers to the interrelation of different species in spatial distribution, reflecting relationship formed by the mutual influence and interaction of various species in different habitats in the community (Gleason 1926, Feroz et al. 2014, Chai et al. 2016). Accordingly, it can reflect the species' spatial distribution relationship and their functional dependency on the environment. Niche and interspecific association, to a great extent, altogether explain the spatial distribution of species and their utilization of environmental resources in

the community (Jiang et al. 2019). Therefore, the joint research on niche and interspecific association of the community will help to better understand the ecological habits of the dominant species on resource utilization and their interrelationships, which will provide a basis for biodiversity conservation and forest management of endangered plant species.

This study examined the niche and interspecific association of dominant tree populations of *Zelkova schneideriana* communities in southern Jiangsu, eastern China. The aim of this study was to provide a theoretical basis for the protection and effective management of this endangered species. More specifically, the following four questions were addressed: (1) What is the status of *Z. schneideriana* populations in the communities? (2) How is *Z. schneideriana*'s ability to exploit environmental resources, compared with other dominant tree species in the communities? (3) What is the interspecific relationship between this species and associated tree species in *Z. schneideriana* communities? (4) What are the implications for the conservation of *Z. schneideriana* based on the results of niche indices and interspecific relationships?

Materials and methods

Study area. The study was in the mountainous area of Liyang and Jintan in Changzhou City (31° 09' - 32° 04' N, 119° 08' - 120° 12' E), which is located in southern Jiangsu Province, eastern China (Figure 1). Changzhou has a northern subtropical monsoon climate, with mild, humid weather and an average annual temperature of 16.3 °C, total annual precipitation of 1,068.9 mm, and an annual frost-free period of 237 d (Yang et al. 2013). The soil is predominantly yellow-brown soil. The vegetation type is mainly deciduous broadleaved forests with few evergreen broadleaved tree species; the dominant species include *Z. schneideriana*, *Celtis sinensis* Pers., *Dalbergia hupeana* Hance, and *Aphananthe aspera* (Thunb.) Planch. In addition, there are some coniferous and broadleaved mixed forests, bamboo forests, and shrublands in the hilly land of Changzhou.

Sampling design. Based on our comprehensive field survey in 2019, three sites were selected for study in a mountain area in southern Jiangsu Province where there was a large distribution area of *Z. schneideriana* forests (Table 1). At each of the three sites, we designated seven 20 × 20 m sampling plots. Thus, a total of 21 plots with a total area of 8,400 m² at three sites were sampled. The forest was

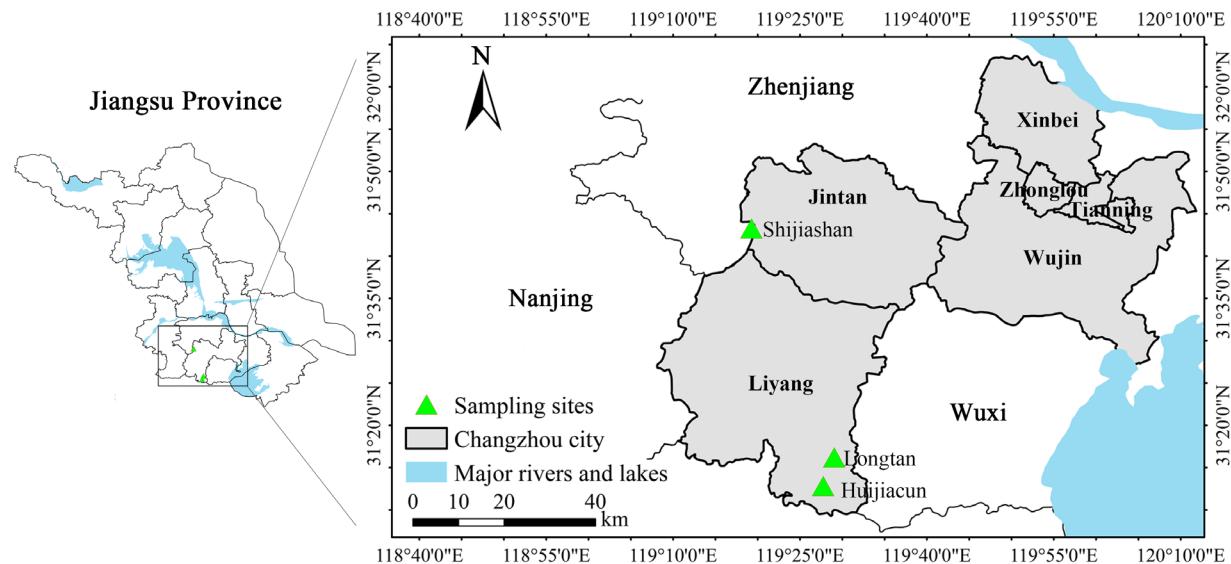


Figure 1. Location map of *Z. schneideriana* sampling sites in southern Jiangsu, eastern China

divided into three layers: tree layer, shrub layer, and herb layer. For the convenience of field investigation, each plot (or quadrat) was divided into four 10×10 m subplots. The tree layer (DBH ≥ 5 cm) was investigated for each species, and species name, tree height, and diameter at breast height (DBH at 1.3 m) were recorded (Li & Zhang 2015). Topographic elements including longitude, latitude, and elevation were also recorded (Table 1).

Importance value. The importance value (IV) can reflect the position and function of species in the community, which was calculated with the following formula (Curtis & McIntosh 1950, Zhang 2011, Li et al. 2020):

$$IV = (RA + RD + RF) / 3$$

$$RA = a_i / \sum_{i=1}^S a_i \quad RD = d_i / \sum_{i=1}^S d_i \quad RF = f_i / \sum_{i=1}^S f_i$$

where IV is the importance value, RA is the relative abundance, RD is the relative dominance, and RF is the relative frequency. a_i is the number of individuals of population i , d_i is the basal area at the height of 1.3 m of population i , f_i is the number of quadrats in which the population i appeared, and S is the total number of species.

Niche breadth. The Levins index and Shannon-Wiener index were used to calculate the niche breadth of the dominant species (the top 10 species in terms of IV) in *Z.*

schneideriana communities (Shannon et al. 1949, Levins 1968, Tian et al. 2018, Lu et al. 2020).

(1) Levins index:

$$B_L = 1 / \sum_{j=1}^r P_{ij}^2$$

(2) Shannon-Wiener index:

$$B_S = - \sum_{j=1}^r P_{ij} \ln P_{ij}$$

where n_{ij} is the importance value of species i in resource j , N_i is the sum of the importance value of species i in all resources ($N_i = \sum_{j=1}^r n_{ij}$), P_{ij} is the proportion of the utilization of resource j by species i in all resources ($P_{ij} = n_{ij} / N_i$), and r is the resource digit, namely the total number of quadrats.

Niche overlap. The niche overlap of the dominant populations in *Z. schneideriana* communities was calculated using the niche similarity index and niche overlap index (Pianka 1973, Schoener 1974, Lu et al. 2020).

(1) Niche similarity index:

$$C_{ik} = 1 - 0.5 \sum_{j=1}^r |P_{ij} - P_{kj}|$$

(2) Niche overlap index:

$$O_{ik} = \sum_{j=1}^r P_{ij} P_{kj} / \sqrt{\sum_{j=1}^r P_{ij}^2 \sum_{j=1}^r P_{kj}^2}$$

Table 1. The basic information of *Z. schneideriana* communities sampled at three sites in southern Jiangsu, eastern China.

Sites	Area (m ²)	Latitude	Longitude	Elevation (m)	Tree density (no./hm ²)	Average DBH of trees (cm/hm ²)
Huijiacun, Liyang	7 (20 × 20)	31° 12' 50" N	119° 27' 44" E	122 - 140	871.43	7289.14
Longtan, Liyang	7 (20 × 20)	31° 16' 13" N	119° 29' 02" E	148 - 160	942.86	7756.93
Shijiashan, Jintan	7 (20 × 20)	31° 43' 16" N	119° 19' 15" E	108 - 130	960.71	5338.42

where C_{ik} and O_{ik} are the niche similarity index and niche overlap index between species i and k respectively; P_{ij} and P_{kj} are the proportion of resources j used by species i or k , respectively.

It is generally regarded that the importance value of each species in a plant community, reflects its utilization of various resources and the spatial relationship relative to other plant species (Zhang *et al.* 2003). In this study, we took the investigated quadrat as the resource status, the quadrat number as the number of resource gradient. Accordingly, we applied the importance value of a species as quantitative index to measure its niche breadth and overlap.

Overall interspecific association. The variance ratio (VR) was used to determine the overall interspecific relationships, and the significance was further tested using the W value. The formula is as follows (Schluter 1984, Wang *et al.* 2019):

$$P_i = n_i / N$$

$$\delta_T^2 = \sum_{i=1}^S P_i(1-P_i), \quad S_T^2 = \frac{1}{N} \sum_{j=1}^N (T_j - t)^2$$

$$VR = S_T^2 / \delta_T^2, \quad W = N \times VR$$

Where n_i is the number of quadrats containing species i , N is the total number of quadrats, δ_T^2 is the variance of total quadrats, S_T^2 is the variance in total species, S is the total number of species, T_j is the number of species occurring in quadrats j , and t is the average number of species in the quadrats.

If $VR = 1$, species have no association because they are assumed independent. Species show a positive association

when $VR > 1$; $VR < 1$ indicates that species have a negative association. The W value was used to test whether the VR value deviated significantly from 1. If $W > \chi^2_{0.05(N)}$ or $W < \chi^2_{0.95(N)}$, the overall interspecific association was significant ($P < 0.05$). Conversely, the overall interspecific association was not significant when $\chi^2_{0.95(N)} < W < \chi^2_{0.05(N)}$ ($P > 0.05$).

Chi-square test. Chi-square (χ^2) was conducted based on a 2×2 contingency table for the qualitative study of interspecific association. Since this study was a discontinuous sample, χ^2 was corrected by Yates' continuous correction formula (Greig-Smith 1983, Dai *et al.* 2020). When the frequency of occurrence of a certain species is 100 %, the b and d values are weighted to 1 in order to avoid a non-computable situation when the denominator is 0 (Jiang *et al.* 2019). The aim is to obtain more objective results. This was calculated as follows:

$$\chi^2 = \frac{N(ad - bc) - 0.5N}{(a+b)(b+d)(c+d)(a+c)}$$

Where N is the total quadrat number, a is the number of quadrats containing species i and k , b is the number of quadrats containing species i but not k , c is the number of quadrats containing species k but not i , and d is the number of quadrats in which neither i nor k is found.

When $\chi^2 < 3.841$, there is no interspecific association ($P > 0.05$); when $3.841 \leq \chi^2 < 6.635$, the interspecific association was significant ($0.01 < P \leq 0.05$). When $\chi^2 \geq 6.635$, the interspecific association was highly significant ($P \leq 0.01$). In addition, if $ad > bc$, there is a positive association and the species pairs tend to appear at the same time. Conversely, if $ad < bc$, there is a negative association and the species pair tends to be independent.

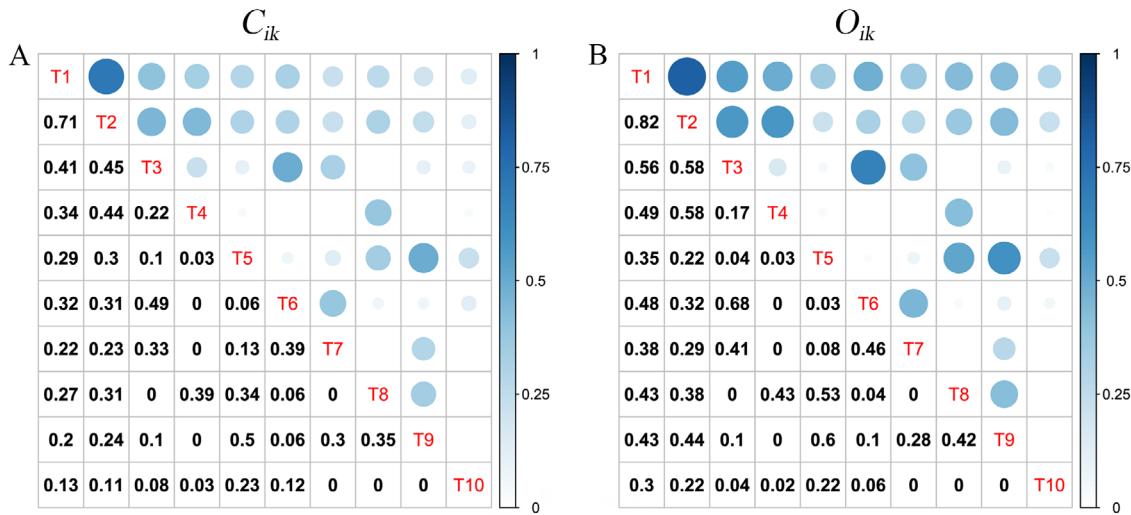


Figure 2. Niche overlap of dominant tree species in *Z. schneideriana* communities in southern Jiangsu, eastern China. (A) Niche similarity index (C_{ik}); (B) niche overlap index (O_{ik}). Tree species code (T1~T10) according to [Table 2](#). The size and color of the circles (above the diagonal) show the value of niche overlap (below the diagonal). Color intensity and the size of the circles are proportional to the absolute value of niche overlap (C_{ik} or O_{ik}).

Spearman's correlation coefficient. Spearman's correlation coefficient of dominant species in *Z. schneideriana* communities was calculated using the following formula ([Spearman 1904](#), [Xu et al. 2016](#), [Huang et al. 2017](#)):

$$r_s(i, k) = 1 - \frac{6 \sum_{j=1}^N (x_{ij} - \bar{x}_i)^2 (x_{kj} - \bar{x}_k)^2}{N^3 - N}$$

Where $r_s(i, k)$ is Spearman's correlation coefficient; N is the total number of quadrats; x_{ij} and x_{ik} is the importance value of species i and k , respectively, in quadrat j ; \bar{x}_i and \bar{x}_k are the average of the importance values of species i and k in all quadrats, respectively.

R 4.0.3 ([R Development Core Team 2020](#)) and Excel 2016 (Microsoft Corporation, USA) were used for all statistical analyses. The “spaa” package was used to analyze niche and interspecific association ([Zhang 2016](#)). In addition, ArcGIS 10.6 (Environmental Systems Research Institute, USA) was used to generate the maps of *Z. schneideriana* sampling plots.

Results

Importance values of dominant species. In our study, the three sites are not far away from each other ([Table 1](#)). Most tree species occurred at several plots, rather than at only one plot. Therefore, we used the *IV* to determine the number of dominant species in the tree layer of the com-

munities. Among the 21 sample plots, there were 39 species belonging to 25 families and 32 genera in the tree layer. The sum of importance value of the 10 most dominant species accounted for 76.64 % (DBH \geq 5 cm); therefore, these ten species were selected as dominant species for niche and interspecific association analyses ([Table 2](#)). In the tree layer, the importance value of *Z. schneideriana* was the highest (37.96), followed by *C. sinensis* (15.02); *Phyllostachys edulis* (Carriere) J. Houzeau had the lowest importance value (1.65). Therefore, there was a striking difference in the *IV* of these species.

Niche breadth of dominant populations. There was a large difference in the niche breadth of the 10 most dominant species in the tree layer of *Z. schneideriana* communities. The Levins index (B_L) ranged from 1.75 to 19.84, while the Shannon-Wiener index (B_S) ranged from 0 to 3.04. In terms of B_L and B_S , *Z. schneideriana* had the highest niche breadth (B_L : 19.84, B_S : 3.02), followed by *C. sinensis* (B_L : 14.80, B_S : 2.77), and *Ph. edulis* had the lowest niche breadth (B_L : 1.75, B_S : 0.77) ([Table 2](#)). For these dominant species, the ranking result of B_L was largely consistent with B_S , except for *Liquidambar formosana* Hance and *Litsea glutinosa* Ait ([Table 2](#)).

Niche overlap of dominant populations. Of the 45 species pairs consisting of 10 dominant species, the niche similarity indices (C_{ik}) ranged from 0.00 to 0.71 and the aver-

Table 2. Importance value and niche breadth of dominant tree species in *Z. schneideriana* communities in southern Jiangsu, eastern China.

No.	Dominant tree species	IV/%	Levins index		Shannon-Wiener index	
			B_L	Ordination	B_s	Ordination
T1	<i>Zelkova schneideriana</i>	37.96	19.84	1	3.02	1
T2	<i>Celtis sinensis</i>	15.02	14.80	2	2.77	2
T3	<i>Dalbergia hupeana</i>	4.77	7.33	3	2.09	3
T4	<i>Aphananthe aspera</i>	4.49	5.76	4	1.88	4
T5	<i>Firmiana simplex</i>	2.92	3.57	8	1.51	8
T6	<i>Liquidambar formosana</i>	2.83	5.20	6	1.78	5
T7	<i>Platycarya strobilacea</i>	2.70	4.17	7	1.51	7
T8	<i>Ligustrum lucidum</i>	2.32	5.24	5	1.72	6
T9	<i>Phoebe sheareri</i>	1.98	3.48	9	1.30	9
T10	<i>Phyllostachys edulis</i>	1.65	1.75	10	0.77	10

Note: IV, importance value; B_L , Levins index; B_s , Shannon-Wiener index. T1, T2, T3, T4, T5, T6, T7, T8, T9, and T10 correspond to *Zelkova schneideriana*, *Celtis sinensis*, *Dalbergia hupeana*, *Aphananthe aspera*, *Firmiana simplex*, *Liquidambar formosana*, *Platycarya strobilacea*, *Ligustrum lucidum*, *Phoebe sheareri*, and *Phyllostachys edulis* respectively. The same below.

age was 0.21. In the tree layer, only one pair with $C_{ik} > 0.5$ was found, accounting for 2.22 % of all species pairs. The other 44 pairs had $C_{ik} \leq 0.5$, accounting for 97.78 %. These findings suggested that there was a considerable difference in the requirements of those species on environmental resources (Figure 2A). The niche overlap index (O_{ik}) ranged from 0.00 to 0.82, and the average was 0.27. Seven pairs with $O_{ik} > 0.5$ were found, accounting for 15.56 %; the other 38 pairs had $O_{ik} \leq 0.5$, accounting for 84.44 % (Figure 2B). Generally, if the niche overlap value was greater than 0.5, it was considered as relatively high; if less than 0.5, it was considered as relatively low (Tian et al. 2018). Similarly, the niche overlap indices (O_{ik}) of most species pairs were also relatively low ($\bar{O}_{ik} = 0.27$), suggesting there was little or no competition among most species in the tree layer of *Z. schneideriana* communities (Figure 2B). In addition, the average C_{ik} and O_{ik} between *Z. schneideriana* and other associated species were 0.32 and 0.47, respectively, and the greatest overlaps were found between *Z. schneideriana* and *C. sinensis* ($C_{ik} = 0.71$, $O_{ik} = 0.82$).

Overall interspecific association. The variance ratio (VR) of the overall interspecific associations among the dominant tree species was 0.80 ($VR < 1$) in the tree layer of *Z. schneideriana* communities, indicating a negative interspecific association. Furthermore, the W value was 16.89 ($\chi^2_{0.95(N)} < W < \chi^2_{0.05(N)}$), indicating that there was no significant interspecific association ($P > 0.05$).

Association between major species pairs. In the χ^2 test, 15 species pairs showed positive associations in the tree layer, among which there was a highly significant difference between one pair and no significant difference between 14 pairs. *Firmiana simplex* (T5) and *Phoebe sheareri* (T9) showed highly significant positive correlation in the χ^2 test. Twenty-eight pairs showed negative associations, among which there were significant differences between two pairs and no significant difference between 26 pairs. The two species pairs namely *Dalbergia hupeana* (T3) and *Ligustrum lucidum* (T8), *Aphananthe aspera* (T4) and *Liquidambar formosana* (T6), presented significantly negative correlation in the χ^2 test. In addition, the remaining two pairs showed no association (Figure 3). The semi-matrix diagram of Spearman's correlation coefficient further revealed that 18 pairs showed positive associations in the tree layer, among which there were highly significant differences in two pairs and no significant difference in 16 pairs. The two species pairs namely *Firmiana simplex* (T5) and *Phoebe sheareri* (T9), *Dalbergia hupeana* (T3) and *Liquidambar formosana* (T6), presented highly significant positive correlation in light of Spearman's correlation coefficient. Twenty-seven pairs showed negative associations, among which there were significant differences between two pairs and no significant difference in 25 pairs (Figure 4). The two species pairs namely *Dalbergia hupeana* (T3) and *Ligustrum lucidum* (T8), *Aphananthe aspera* (T4) and *Liquidambar formosana* (T6), presented

significantly negative correlation in light of Spearman's correlation coefficient.

In the tree layer of *Z. schneideriana* communities, the results of the χ^2 test and Spearman's correlation coefficient showed that the species pairs were more negatively associated than positively associated, which was consistent with the results of the overall interspecific association analysis. The results showed that most associations between pairs of species were not statistically significant.

Discussion

Importance values and niche breadth. Importance value and niche breadth are comprehensive indices that can be used to measure the role and status of species in a community, but the two indices have different ecological significance. The importance value reflects the status, advantage, and function of species in the community, whereas niche breadth evaluates the ability of a species to utilize environmental resources (Liu et al. 2018, Tian et al. 2018). Our results showed that *Z. schneideriana* had the highest importance value and niche breadth, indicating that *Z. schneideriana* was the most important dominant species. In general, the dominant species in dominant layer is commonly known as the instructive species in a forest community (Zhou 2010). Our investigation shows that *Z. schneideriana* communities can be divided into three layers: tree layer, shrub layer and herb layer. *Z. schneideriana* in the

tree layer had the *IV* of 37.97 (Table 2), taking almost half of the total *IV* of the first ten tree species. This indicates that *Z. schneideriana* was an instructive species or edifier tree. *Z. schneideriana* made full use of environmental resources and had strong environmental adaptability, thus, playing a significant role in the stability and composition of the communities in the sampled locations. In contrast, the importance values and niche breadth of other species were relatively low, indicating that their adaptability and ability to utilize local resources were poor. Consequently, their distributions were relatively narrow. For example, *Phoebe shearerii* (Hemsl.) Gamble, an evergreen tree endemic to China (Ding et al. 2018), was typically found in valleys in the study area.

Niche overlap and interspecific association. Interspecific association and niche overlap are closely correlated. Many studies have shown that a positive association indicates the use of similar resources and a niche overlap, whereas a negative association indicates that species have different habitat and resource requirements (Su et al. 2015, Gu et al. 2017, Li et al. 2017). In this study, both *Z. schneideriana* and *C. sinensis* had a positive association, with a large overlap in habitat and niche, which may be related to the fact that both species are sun-loving deciduous trees. In contrast, *D. hupeana* and *L. lucidum* are deciduous and evergreen trees, respectively, but *L. lucidum* is more salt-tolerant than *D. hupeana* (Su et al. 2011, Lai et al. 2020). As a result, *D. hupeana* and *L. lucidum* had a negative association and had a minimal shared niche and habitat.

Niche overlap and interspecific association reflect the degree of interspecific competition and community stability (Moloney & Levin 1996, Wu et al. 2013). In the tree layer of *Z. schneideriana* communities, the niche similarity and niche overlap indices of most species were relatively low, which indicated that the competition among these species was not intense due to their different demands for environmental resources. At the same time, the overall interspecific association showed negative association that was not significantly different demonstrating that most tree species were relatively independent and less likely to be affected by other co-occurring species. Based on the χ^2 test and Spearman's correlation coefficient, most species pairs exhibited no significant correlation and the number of negatively associated species pairs was greater than positively associated species pairs, which was consistent with the overall interspecific results. As such, we hypothesize that dominant species of tree layer is relatively independent during the early stage of forest community

T1												
T2												
T3												
T4												
T5	0.01	0.24	0.00	0.61								
T6	0.05	0.44	1.97	4.27*	0.26							
T7	0.00	0.10	1.97	2.20	0.01	0.82						
T8	0.01	0.24	4.09*	1.46	0.05	0.26	1.11					
T9	0.03	0.01	0.06	1.37	8.41**	0.04	0.51	0.19				
T10	0.13	0.02	0.07	0.21	0.79	0.44	0.10	0.24	0.01			

Figure 3. χ^2 test of dominant tree species in *Z. schneideriana* communities in southern Jiangsu, eastern China. Blue, red, and white color represents positive association (*VR* > 0, 15 pairs), negative association (*VR* < 0, 28 pairs) and no association (*VR* = 0, 2 pairs), respectively. Species codes in the diagonal are the same as in Table 2. *: $P < 0.05$, **: $P < 0.01$.

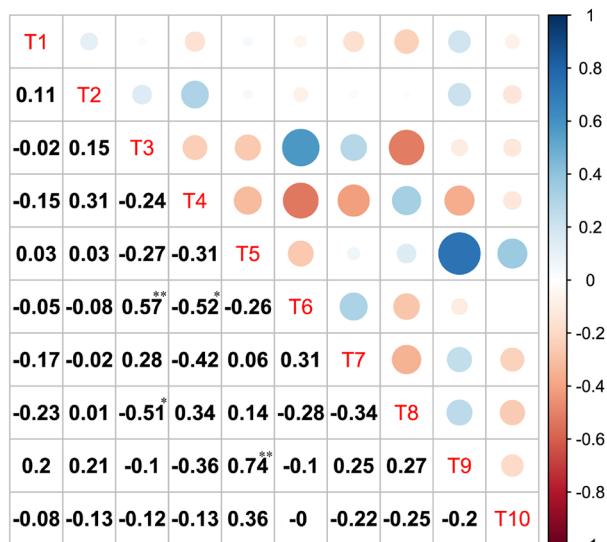


Figure 4. Spearman's correlation coefficient of dominant tree species in *Z. schneideriana* communities in southern Jiangsu, eastern China. Tree species code (T1~T10) according to Table 2. The size and color of the circles (above the diagonal) show the value of Spearman's correlation coefficient (below the diagonal). Blue and red color represents positive association (18 pairs), negative association (27 pairs) respectively. Color intensity and the size of the circles are proportional to the absolute value of Spearman's correlation coefficient *: $P < 0.05$; **: $P < 0.01$.

succession in subtropical China. However, with succession proceeding, the communities may gradually become stable and more species pairs may exhibit positive associations (Zhang et al. 2016, Gao et al. 2017, Liu et al. 2017).

Besides, the niche overlap between *Z. schneideriana* and *C. sinensis* is the greatest in terms of C_{ik} or O_{ik} (Figure 2) among the 45 species pairs. This indicates that both species may have relatively consistent requirements for environmental resources. When environmental resources are insufficient, intense competition may occur between these two species.

Implications for conservation. Our results indicate that most of the dominant tree species in the *Z. schneideriana* communities exhibited a distinctive demand for resources, with little competition, and the species were only slightly associated or even independent. At present, except for the Huijiacun population, the Longtan population is protected due to its location in Tianmu National Forest Park, Jiangsu Province, and the Shijiashan population was protected because it was located in a small nature reserve for endangered plant species. According to the genetic analysis, most variation consistently originated from within *Z.*

schneideriana population, whereas its genetic differentiation among population was not significant (Liu et al. 2005, Liu et al. 2016). Therefore, we suggest establishing a small nature reserve to protect the wild population in Huijiacun.

Our results also indicate that most of the interspecific associations between *Z. schneideriana* and its co-occurring tree species were primarily negative. Recent research has found that *Z. schneideriana* had long seed dormancy, a high empty-nut ratio, and low maximum net photosynthetic rate (Shen et al. 2011, Zhang et al. 2013, Tian et al. 2014). Although *Z. schneideriana* currently occupies a dominant position in the stand, the relationship between its population and other associated tree species may change with the continued ecological succession. In other words, the competition between species may intensify in the future. Thus, we recommended conducting dynamic monitoring in these dominant populations of *Z. schneideriana* communities.

In summary, our study is the first to show the niche characteristics and interspecific associations of the dominant species in *Z. schneideriana* communities. Based on the importance value and niche breadth, *Z. schneideriana* was the constructive species or edifier tree in the investigated communities. We also found that dissimilarity in environmental requirements existed among most dominant tree species, thus, decreasing interspecific competition. This is likely due to the instability of the *Z. schneideriana* community because it is in the early stages of succession. In addition, we suggest strengthening the population conservation of *Z. schneideriana* by establishing a small nature reserve and by conducting dynamic monitoring of these dominant populations in the investigated communities.

Acknowledgments

We thank Rui Yao, Xianli Peng, and Qian Li for their cooperation with our field survey. This paper was financially supported by Top-notch Academic Programs Project of Jiangsu Higher Education Institutions (TAPP).

Literature cited

- Bai XH, Zhang JT. 2017. Niche analysis of dominant species of forest community in Xiaowutai Mountain, China. *Chinese Journal of Applied Ecology* 28: 3815-3826. DOI: <https://doi.org/10.13287/j.1001-9332.201712.002>

- Chai ZZ, Sun CL, Wang DX, Liu WZ. 2016. Interspecific associations of dominant tree populations in a virgin old-growth oak forest in the Qinling Mountains, China. *Botanical Studies* **57**: 23. DOI: <https://doi.org/10.1186/s40529-016-0139-5>
- Colwell RK, Futuyma DJ. 1971. On the measurement of niche breadth and overlap. *Ecology* **52**: 567-576. DOI: <https://doi.org/10.2307/1934144>
- Curtis JT, McIntosh RP. 1950. The interrelations of certain analytic and synthetic phytosociological characters. *Ecology* **31**: 434-455. DOI: <https://doi.org/10.2307/1931497>
- Dai JY, Liu HY, Xu CY, Qi Y, Zhu XR, Zhou M, Liu BB, Wu YH. 2020. Divergent hydraulic strategies explain the interspecific associations of co-occurring trees in forest-steppe ecotone. *Forests* **11**: 1-12. DOI: <https://doi.org/10.3390/f11090942>
- Denk T, Grimm GW. 2015. Phylogeny and biogeography of *Zelkova* (Ulmaceae *sensu stricto*) as inferred from leaf morphology, ITS sequence data and the fossil record. *Botanical Journal of the Linnean Society* **147**: 129-157. DOI: <https://doi.org/10.1111/j.1095-8339.2005.00354.x>
- Ding W, Ning LP, Li M, Shi H, An RM, Wang TS. 2018. Chemical constituents of the essential oil extracted from *Phoebe sheareri*. *Chemistry of Natural Compounds* **54**: 1-2. DOI: <https://doi.org/10.1007/s10600-018-2294-2>
- Feroz SM, Alam MR, Das P, Mamun AA. 2014. Community ecology and spatial distribution of trees in a tropical wet evergreen forest in Kaptai National Park in Chittagong Hill Tracts, Bangladesh. *Journal of Forestry Research* **25**: 311-318. DOI: <https://doi.org/10.1007/s11676-013-0423-0>
- Gao HJ, Yuan J, Gao PS. 2017. Niche and interspecific association of dominant species in secondary forest of Zhoushan Islands. *Journal of Tropical and Subtropical Botany* **25**: 73-80. DOI: <https://doi.org/10.11926/jtsb.3620>
- Gleason HA. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* **53**: 7-26. DOI: <https://doi.org/10.2307/2479933>
- Greig-Smith P. 1983. *Quantitative Plant Ecology*. Oxford: Blackwell Scientific Publications. ISBN: 0-520-05080-0
- Grinnell J. 1917. The niche-relationship of the *California Thrasher*. *The Auk* **34**: 427-433. DOI: <https://doi.org/10.2307/4072271>
- Gu L, Gong ZW, Li WZ. 2017. Niches and interspecific associations of dominant populations in three changed stages of natural secondary forests on Loess Plateau, P. R. China. *Scientific Reports* **7**: 1-12. DOI: <https://doi.org/10.1038/s41598-017-06689-9>
- Huang YY, Han H, Tang C, Liu SJ. 2017. Plant community composition and interspecific relationships among dominant species on a post-seismic landslide in Hongchun Gully, China. *Journal of Mountain Science* **14**: 1985-1994. DOI: <https://doi.org/10.1007/s11629-017-4382-3>
- Jiang H, Zhang H, Long WX, Fang YS, Fu MQ, Zhu KX. 2019. Interspecific associations and niche characteristics of communities invaded by *Decalobanthus boissianus*. *Biodiversity Science* **27**: 388-399. DOI: <https://doi.org/10.17520/biods.2019007>
- Jiangsu Forestry Bureau. 2017. *The Key Protected Wild Plants in Jiangsu Province*. Nanjing: Nanjing Normal University Press. ISBN: 978-7-5651-3567-5
- Jin XL, Zhang RQ, Zhang DL, He P, Cao FX. 2009. *In vitro* plant regeneration of *Zelkova schneideriana*, an endangered woody species in China, from leaf explants. *The Journal of Horticultural Science and Biotechnology* **84**: 415-420. DOI: <https://doi.org/10.1080/14620316.2009.11512542>
- Lai XL, Yan YJ, Yan LH. 2020. Effects of NaCl stress on growth and physiological characteristics of *Dalbergia hupeana* seedlings. *Plant Physiology Journal* **56**: 309-316. DOI: <https://doi.org/10.13592/j.cnki.ppj.2019.0152>
- Levins R. 1968. *Evolution in Changing Environments: Some Theoretical Explorations*. Princeton: Princeton University Press. ISBN: 9780691080628
- Li L, Wei SG, Lian JY, Cao HL. 2020. Distributional regularity of species diversity in plant community at different latitudes in subtropics. *Acta Ecologica Sinica* **40**: 1249-1257. DOI: <https://doi.org/10.5846/stxb201812012615>
- Li W, Zhang GF. 2015. Population structure and spatial pattern of the endemic and endangered subtropical tree *Parrotia subaequalis* (Hamamelidaceae). *Flora* **212**: 10-18. DOI: <https://doi.org/10.1016/j.flora.2015.02.002>
- Li QL, Zong XH, Deng HP, Wang HX, Wu HY, Liang S, Liu BY. 2017. Niche and interspecific association of dominant species in tree layer of Chishui *Alsophila spinulosa* community. *Acta Botanica Boreali-Occidentalis Sinica* **37**: 1422-1428. DOI: <https://doi.org/10.7606/j.issn.1000-4025.2017.07>
- Liu RH, Jiang Y, Chang B, Li JF, Rong CY, Liang SC, Yang RA, Liu XT, Zeng HF, Su XL, Yuan HY, Fu GH,

- Wu YH. 2018. Interspecific associations and correlations among the main woody plants in a *Pterocarya stenoptera* community in a riparian zone of Lijiang River, Guilin, Southwest China. *Acta Ecologica Sinica* **29**: 3917-3926. DOI: <https://doi.org/10.5846/stxb201802270396>
- Liu XC, Li YY, Chen SY. 2005. Genetic diversity of *Zelkova schneideriana* from different provenance by ISSR analysis. *Yunnan Forestry and Technology* **34**: 43-47. DOI: <https://doi.org/10.3969/j.issn.1672-8246.2005.02.008>
- Liu LT, Wang XD, Wen Q, Jia QQ, Liu QJ. 2017. Interspecific associations of plant populations in rare earth mining wasteland in southern China. *International Biodeterioration & Biodegradation* **118**: 82-88. DOI: <https://doi.org/10.1016/j.ibiod.2017.01.011>
- Liu HL, Zhang RQ, Geng ML, Zhu JY, An JC, Ma JL. 2016. Chloroplast analysis of *Zelkova schneideriana* (Ulmaceae): genetic diversity, population structure, and conservation implications. *Genetics and Molecular Research* **15**: 1-9. DOI: <https://doi.org/10.4238/gmr.15017739>
- Lu YP, Chen W, Yao J, Huang YQ, Zhang Y, Liu HC, He XY. 2020. Multiple spatial scale analysis of the niche characteristics of the *Rhododendron dauricum* plant communities in northeast China. *Chinese Geographical Science* **3**: 614-630. DOI: <https://doi.org/10.1007/s11769-020-1138-8>
- Ma F, Zhang JL. 2009. *Investigation on Key Protected Wild Plant Resources in China*. Beijing: China Forestry Publishing House. ISBN: 978-7-5038-5137-7
- Moloney KA, Levin SA. 1996. The effects of disturbance architecture on landscape-level population dynamics. *Ecology* **77**: 375-394. DOI: <https://doi.org/10.2307/2265616>
- Pianka ER. 1973. The structure of lizard community. *Annual Review of Ecology and Systematics* **4**: 53-74. DOI: <https://doi.org/10.1146/annurev.es.04.110173.000413>
- R Development Core Team. 2020. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Schlüter D. 1984. A variance test for detecting species associations, with some example applications. *Ecology* **65**: 998-1005. DOI: <https://doi.org/10.2307/1938071>
- Schoener TW. 1974. Resource partitioning in ecological communities. *Science* **185**: 27-39. DOI: <https://doi.org/10.1126/science.185.4145.27>
- Shannon CE, Weaver W, Wiener N. 1949. *The Mathematical Theory of Communication*. Urbana: University of Illinois Press. ISBN: 9780252725487
- Shen JJ, Bai ME, Huang XB, Yu GP, Feng XY. 2011. Studies on morphology and germination characteristics of *Zelkova schneideriana*. *Journal of Zhejiang Forestry and Technology* **31**: 56-59. DOI: <https://doi.org/10.3969/j.issn.1001-3776.2011.06.011>
- Spearman C. 1904. The proof and measurement of association between two things. *The American Journal of Psychology* **15**: 72-101. DOI: <https://doi.org/10.2307/1412159>
- Su SJ, Liu JF, He ZS, Zheng SQ, Hong W, Xu DW. 2015. Ecological species groups and interspecific association of dominant tree species in Daiyun Mountain National Nature Reserve. *Journal of Mountain Science* **12**: 637-646. DOI: <https://doi.org/10.1007/s11629-013-2935-7>
- Su WG, Wang XQ, Gao YY. 2011. Influence of salt-stress on the landscape plant *Ligustrum lucidum*. *Journal of Anhui Agriculture* **39**: 10881-10898. DOI: <https://doi.org/10.13989/j.cnki.0517-6611.2011.18.201>
- Tian YC, Cao SJ, Cao JW. 2014. Study on morphology and germination characteristics of seeds of six species of *Zelkova schneideriana*. *Northern Horticulture* **11**: 71-74. DOI: <https://doi.org/CNKI:SUN:BFYY.0.2014-11-025>
- Tian ZQ, Li HC, Li WY, Gan XH, Zhang XM, Fan ZL. 2018. Structural characteristics and niches of dominant tree populations in *Tetracentron sinense* communities: Implications for conservation. *Botanical Sciences* **96**: 157-167. DOI: <https://doi.org/10.17129/botsci.1531>
- Wang YF, Ferguson DK, Zetter R, Denk T, Garfi G. 2001. Leaf architecture and epidermal characters in *Zelkova*, Ulmaceae. *Botanical Journal of the Linnean Society* **136**: 255-265. DOI: <https://doi.org/10.1006/bjol.2000.0432>
- Wang Q, Zhu RB, Cheng JM, Deng ZX, Guan WB, El-Kassaby YA. 2019. Species association in *Xanthoceras sorbifolium* Bunge communities and selection for agroforestry establishment. *Agroforestry Systems* **93**: 1531-1543. DOI: <https://doi.org/10.1007/s10457-018-0265-z>
- Wu ZY, Raven PH. 2003. *Flora of China (Vol.5)*. Beijing: Science Press. ISBN: 7-03-012295-X/Q1324
- Wu XJ, Zhang ZW, Meng XF, Li Z, Wang YJ. 2013. Dynamics of diversity, distribution patterns and interspecific associations of understory herbs in the city-suburb-exurb context of Wuhan City, China. *Archives of Biological Sciences* **4**: 1619-1628. DOI: <https://doi.org/10.2298/ABS1304619W>

- Xu MH, Liu M, Zhai DT, Liu T. 2016. A review of contents and methods used to analyze various aspects of plant interspecific associations. *Acta Ecologica Sinica* **36**: 8224-8233. DOI: <https://doi.org/10.5846/stxb201505311092>
- Yang WR, Li F, Wang RS, Xiong XX, Liu AS. 2013. Eco-service efficiency assessment method of urban land use: a case study of Changzhou City, China. *Acta Ecologica Sinica* **33**: 4486-4494. DOI: <https://doi.org/10.5846/stxb201204190568>
- Yin H. 2013. *Rare and Endangered Plants in China*. Beijing: China Forestry Publishing House. ISBN: 978-7-5038-7026-2
- Yu SJ, Li Y, Li XC. 2015. An experiment on natural seedling cultivation for *Zelkova schneideriana*. *China Forestry and Technology* **29**: 53-55. DOI: <https://doi.org/10.13360/j.issn.1000-8101.2015.02.012>
- Zhang JT. 2011. *Quantitative Ecology*. Beijing: Science Press. ISBN: 978-7-03-030937-2
- Zhang JL. 2016. *Spaa: Species Association Analysis*. R package version 0.2.2. <https://CRAN.R-project.org/package=spaa> (accessed June 1, 2020)
- Zhang J, Shi YJ, Zhu YQ, Liu EB, Li M, Zhou JP, Li JG. 2013. The photosynthetic carbon fixation characteristics of common tree species in northern Zhejiang. *Acta Ecologica Sinica* **33**: 1740-1750. DOI: <https://doi.org/10.5846/stxb201207130989>
- Zhang XB, Yao R, Zhang GF. 2016. Interspecific relationships of dominant species from *Celtis sinensis* communities in Laoshan National Forest Park, Nanjing. *Journal of Nanjing Normal University (Natural Science Edition)* **39**: 56-64. DOI: <https://doi.org/10.3969/j.issn.1001-4616.2016.04.011>
- Zhang JY, Zhao HL, Zhang TH, Zhao XY. 2003. Niche dynamics of main populations of plants communities in the restoring succession process in Horqin Sandy Land. *Acta Ecologica Sinica* **12**: 2741-2746. DOI: <https://doi.org/10.3321/j.issn:1000-0933.2003.12.030>
- Zhou CF. 2010. *Fundamentals of Ecology*. Beijing: Higher Education Press. ISBN: 978-7-04-029137-7

Associate editor: Pablo Cuevas Reyes

Author contributions: Guangfu Zhang designed research, and did major revision to the manuscript. Liyuan Shao analyzed data and drafted the manuscript. Both performed research.