

# Species-Habitat Associations in a Northern Temperate Forest in China

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This contribution identifies species-habitat associations in a temperate forest in north-eastern China, based on the assumption that habitats are spatially autocorrelated and species are spatially aggregated due to limited seed dispersal. The empirical observations were obtained in a large permanent experimental area covering 660×320 m. The experimental area was subdivided into four habitat types using multivariate regression tree (MRT) analysis. According to an indicator species analysis, 38 of the 47 studied species were found to be significant indicators of the MRT habitat types. The relationships between species richness and topographic variables were found to be scale-dependent, while the great majority of the species shows distinct habitat-dependence. There are 188 potential species-habitat associations, and 114 of these were significantly positive or negative based on habitat randomization. We identified 139 significant associations using a species randomization. A habitat is not a closed system it may be both, either a sink or a source. Therefore, additional to the randomization, the Poisson Cluster Model (PCM) was applied. PCM considers the spatial autocorrelation of species and habitats, and thus appears to be more realistic than the traditional randomization processes. It identified only 37 associations that were significant. In conclusion, the deviation from the random process, i.e. the high degree of species spatial mingling may be explained by persistent immigration across habitats.

**Keywords** dispersal limitations, indicator species, spatial autocorrelation, species richness, topographic differentiation

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## 1 Introduction

Spatial distributions of forest trees often exhibit patterns correlating with the variation of soil chemistry or topography in tropical forests (Harms et al. 2001, Itoh et al. 2003, Russo et al. 2005, Yamada et al. 2006, 2007, John et al. 2007) and in temperate forests (Zhang et al. 2009, 2010). This suggests that the ecological organization caused by niche differentiation may be important for maintaining species diversity and species coexistence. If environmentally biased spatial distributions principally result from niche differentiation, plant species should show particular habitat preferences. They would preferably occur in localities where they have competitive advantages, although spatial autocorrelation cannot be ignored when considering species-habitat associations (Legendre and Legendre 1998).

A common assumption of most traditional statistical methods for species-habitat associations is that individuals are independently distributed with respect to conspecifics (Condit 1996, Clark et al. 1998, Plotkin et al. 2000). But the independence assumption is often violated by the patterns produced by short-distance dispersal and recruitment processes. The limited dispersal of seeds and short-distance recruitments would contribute to the spatial autocorrelation of species distributions (Condit 1996, Clark et al. 1998, Plotkin et al. 2000). Thus, the assumptions of independence of sample units are often violated by the pattern caused by the dispersal limitations and dependent recruitment processes of trees and shrubs.

To test the contribution of habitat specialization to species coexistence, the relationships between the species spatial distribution and environmental factors need to be studied. In the northern temperate forests of China, the distribution patterns of individuals within a plant population generally tend to be more aggregated than random (Zhang et al. 2009). Furthermore, significant correlations between species and soil nutrients were found in these forests (Zhang et al. 2010). This suggests that habitat preferences are potentially important in explaining the spatial variation in tree communities. Nakashizuka (2001) maintained that habitat specialization remains a prominent hypothesis to explain the species coexistence in a temperate forest community.

The objective of this study is to analyse some of the mechanisms generating differences in species abundance across habitat types. The fully mapped experimental area of 21 ha is located in a multi-species forest ecosystem in North-Eastern China. We assume that habitats are spatially auto-correlated and that the range of seed dispersal is limited. Based on previous field observations, we expect substantial species-habitat associations in the experimental area. Specific objectives of this study are (1) to determine possible scale-dependent associations between species richness and topographic variables; (2) to identify indicator species for a particular habitat and (3) to examine possible associations of trees and shrubs with distinct habitats. We will also discuss the effect of habitat differentiation in maintaining a high species diversity in the *Jiaohe* temperate forest.

## 2 Materials and Methods

### 2.1 Study Area

This study is based on a dataset obtained in a large permanent field plot. The experimental site is located at (43°57.897' ~ 43°58.263' N, 127°42.789' ~ 127°43.310' E) in the *Jiaohe* Management Bureau of the Forest Experimental Zone in Jilin province, in Northeastern China. The research plot measures 320 m × 660 m and covers an area of 21.12 hectares. The altitude in the experimental area ranges from 425.3 m to 525.8 m above sea level. In the study area, the average annual temperature is 3.8 °C. And the hottest month is July with an average day temperature of 21.7 °C. The coldest month is January with an average day temperature of -18.6 °C. The average annual precipitation is 695.9 mm. The soil is a brown forest soil with a rootable depth ranging between 20 and 100 cm. The last recorded tree felling activities took place 50 years ago. The vegetation type represents a mixed broadleaf-conifer forest with 63 species (including three climber species).

Altogether 53916 individual trees with a breast height diameter (dbh) exceeding 1 cm were tagged and mapped, and their species was identified. The dbh value was measured at 1.3 m above ground level. Among the 63 woody species in

the research plot there are 47 abundant species, comprising at least one individual/ha. The species were identified according to the records in the Chinese Virtual Herbarium (see <http://www.cvh.org.cn/cms/>).

The dominant tree species are *Ulmus davidiana* var. *japonica* (Rehder) Nakai, *Pinus koraiensis* Siebold & Zucc., *Juglans mandshurica* Maxim., *Tilia mandshurica* Rupr. et Maxim., *Carpinus cordata* Bl., *Acer mono* Maxim., *Fraxinus mandshurica* Rupr., *Tilia amurense* Rupr. and *Ulmus laciniata* (Trautv.) Mayr. The top five species in stem density are *Acer mandshuricum* Maxim., *Syringa reticulata* var. *amurensis* (Rupr.), *Ulmus davidiana* var. *japonica*, *Carpinus cordata* and *Acer mono*, respectively. The total basal area of dominant tree species and stem density of the top five species are shown in Appendix 1 and 2.

## 2.2 Relationships between Species Richness and Topography

The relative heights at the four corner nodes of each 20 m × 20 m cell were used to develop a variogram model of the entire research area. To examine the association between species richness and topographic variables at different scales, the altitude values were estimated for different cell sizes (5 m × 5 m, 10 m × 10 m, 30 m × 30 m, 40 m × 40 m and 50 m × 50 m) using block kriging (Legendre and Legendre 1998). Species richness in each cell was counted at each of these six different scales. Spearman rank correlation coefficients were calculated to test the relationships between species richness and the topographic variables at each of the six spatial scales. When the plot was subdivided into equally dimensioned cells, the intersections of grid lines were called “nodes”. The relative height differences among the nodes and the elevation of the starting node were measured. Thus it was possible to calculate the elevation of other nodes according to the height difference among nodes and the measured elevation of the starting node. The present study mainly focuses on the results of the 20 m × 20 m cell analysis.

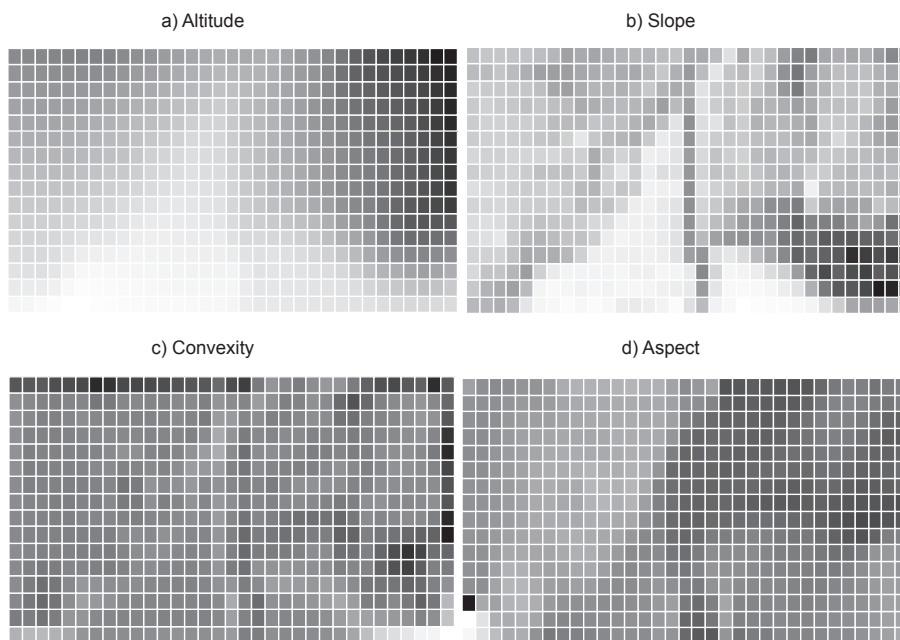
The elevation of a particular cell was calculated as the mean of the elevations of its four corner nodes. The cell slope for each of the five cell sizes was estimated as the mean angular deviation from

the horizontal plane of each of the four triangular planes which were formed by connecting three of its adjacent corners (Harms et al. 2001). The convexity of a cell was calculated as the elevation of the focal cell minus the mean elevation of the eight surrounding cells (cf. Yamakura et al. 1995). For the edge cells, convexity was taken as the elevation of the center point minus the mean of the four corners. Positive and negative convexity values respectively indicate convex (ridge) and concave (valley) land surfaces. The aspect of a cell can be obtained from the average angle of the four triangular planes that deviate from the north direction. Four maps show the spatial pattern of the four topographic variables using 20 m × 20 m cells (Fig. 1). Each cell shows the altitude (ranging from 425.3 m to 525.8 m above sea level with 100.5 m difference in altitude between the highest and lowest cells), the convexity (ranging from -6.6 m to 4.7 m), the slope (ranging from 1.4° to 39.2°) and the aspect (ranging from 41.9° to 329.7°).

## 2.3 Habitat Classification and Indicator Species

Multivariate regression tree (MRT) analysis was performed, following De'ath (2002), to classify habitat types according to topographic conditions and species composition. Distance-based MRT is a relatively new statistical technique that can be used to describe relationships between multi-species data and environmental characteristics. The dissimilarities used in distance-based MRT are calculated by Euclidean distances. Thus, one obtains clusters of sites by repeated splitting of the data, which are chosen to minimize the dissimilarity of sites within clusters.

Habitats were delineated using threshold values for the topographic variables, while the species data was used to find the best thresholds. Indicator values and associated probabilities were computed to identify the statistically significant indicator species in a specific habitat type. Indicator species analysis combines a species relative abundance with its relative frequency of occurrence in the various groups of sites. Indicator value ( $d_{i,c}$ ) of species was calculated as the product of the relative frequency ( $f_{i,c}$ ) and relative average abundance ( $a_{i,c}$ ) in clusters.



**Fig. 1.** Maps depicting four topographic variables at the scale of 20×20 m cells. a) Altitude from 425.3 m (white) to 525.8 m (black) above sea level; b) Convexity from -6.6 m (white) to 4.7 m (black); c) Slope from 1.4° (white) to 39.2° (black); d) Aspect from 41.9° (white) to 329.7° (black).

For cluster  $c$  in set  $K$ :

$$\begin{aligned}
 f_{i,c} &= \frac{\sum_{j \in c} p_{i,j}}{n_c} \\
 a_{i,c} &= \frac{(\sum_{j \in c} x_{i,j}) / n_c}{\sum_{k=1}^K ((\sum_{j \in k} x_{i,j}) / n_k)} \\
 d_{i,c} &= f_{i,c} \times a_{i,c}
 \end{aligned}
 \tag{1}$$

where

$p_{i,j}$  = presence/absence (1/0) of species  $i$  in sample  $j$

$x_{i,j}$  = abundance of species  $i$  in sample  $j$

$n_c$  = number of samples in cluster  $c$

The species indicator value is a maximum when all individuals of a species are found in a single group of sites and when the species occurs in all sites of that group. The statistical significance of the species indicator values is evaluated using a randomization procedure (Dufrière and Legendre 1997). All calculations were done using the  $R$  statistical software (R Development Core Team

2010). MRT analysis was implemented using the “mvpart” library of  $R$  (De’ath 2010). Indicator species analysis was performed using  $R$ ’s “labdsv” library (Roberts 2010).

Rare species with less than 50 individuals within the 21.12 ha study area were excluded from the species–habitat association analysis. Trees at different life stages may have different ecological habitat preferences, as reported by Webb and Peart (2000), Comita et al. (2007) and Lai et al. (2009). In this study, we only focus on the relationship between species types and habitat types. Thus we assume that all individuals of a given species respond similarly to a specific habitat type, regardless of their stage of development.

## 2.4 Testing Species-Habitat Associations

Most methods for testing species-habitat associations assume that trees and shrubs are independently distributed with regard to conspecific individuals. However, the assumption of inde-

pendence is often violated because of the limited range of seed dispersal and recruitment (Harms et al. 2001). In this study, we are using three methods to test this assumption. This study mainly focuses on the results based on a Poisson Cluster Model (PCM) analysis.

#### 2.4.1 Randomized Habitat Maps

This section presents the case where randomized habitat processes were modeled with dispersal limitations of species but no spatially autocorrelated habitat features. Random habitat processes were used to simulate habitat maps that were not autocorrelated. The true species map was used to indicate the dispersal limitations of species.

Spatial dependency within species was evaluated by generating a series of random habitat maps. In these simulated maps the non-overlapping areas are identical in extent to the four habitat types of the true maps. Each simulated map included exactly 248 cells (20 m × 20 m) of habitat type 1, 85 cells of habitat type 2, 52 of habitat type 3 and 143 of habitat type 4. The habitat types were randomly permuted among the 528 cells.

To assess the species associations, each simulated habitat map was matched with the true tree distribution map. Then the relative stem density of the focal species in each habitat type was counted. This procedure was repeated 10000 times. Thus, the frequency distributions of the stem density estimates for each species in each habitat type were obtained from 10000 simulated habitat maps. We then compared the relative stem density of a particular species calculated from the true habitat map with that from the simulated habitat maps. If the proportion of instances where {stem density of simulated habitat maps < stem density of true habitat map} was greater than 0.975, we assumed that the given species was positively associated with a particular habitat at the 0.05 level in a two-tailed test. Alternatively, if the proportion of instances where {stem density of simulated habitat maps > stem density of true habitat map} was greater than 0.975, we assumed that the given species was negatively associated with a particular habitat at the 0.05 level in the two-tailed test.

#### 2.4.2 Randomized Species Maps

This section presents the case where randomized species processes were modeled with no dispersal limitations of species but spatially autocorrelated habitat features. A complete spatial randomness (CSR) process was used to simulate no dispersal limitations of species. The true habitat map was used to indicate spatially autocorrelated habitats.

Spatial dependency within habitat types was tested by generating a series of maps with random locations for each species, using the CSR process in the simulated species maps. Matching the true habitat map with the simulated species maps, we calculate the stem density of each species in each habitat type. This procedure was repeated 10,000 times to establish the frequency distribution of the estimated stem density. Significant deviations of the observed density values from the expected ones were assessed at 0.05 levels using a two-tailed test.

#### 2.4.3 Poisson Cluster Process

Using poisson cluster processes, dispersal limitations of species and spatial autocorrelation of habitat maps were modeled. The Poisson Cluster Model (PCM) was used to simulate the dispersal limitations of species. The true habitat map was used to indicate spatially autocorrelated habitats.

In a subsequent analysis, using Ripley's  $K$  function, it was found that 47 species (Appendix 3) were not randomly distributed, but significantly aggregated. By choosing the PCM approach, it was implied that clusters arise from local propagation. The PCM models aggregation caused by local seed dispersal or gap recruitment. Thus, it was decided to simulate the spatial distribution of each of these species using the Poisson cluster process. The observed spatial aggregation is then used to develop expected species-habitat associations.

Subsequently, we model the spatial aggregation of the species distributions using the PCM with Ripley's  $K$  value as guiding parameter, as recommended by Diggle (1983), Plotkin et al. (2000) and John et al. (2007). The PCM model can be used to capture small-scale spatial aggregation in species distributions that are due to aggregated dispersal (Potts et al., 2004). The definition and parameter

estimation of the Poisson cluster process follows Plotkin et al. (2000).

### 3 Results

#### 3.1 Species Richness and Topography

The correlation between species richness and topography shows a distinct scale-dependence (Table 1). Highly significant or significant negative associations between species richness and altitude were found at finer scales, ranging from 5 m to 30 m, but vanished at higher scales. This result may not be very surprising, considering that fewer species will be able to establish themselves on the rather exposed higher altitudes. The correlations are very weak although significant. It means that there was almost no linear relationship between the studied habitat characteristics and species richness. Thus, some other factors than the studied ones may explain better the species richness or the species richness is affected by many factors each having a low impact alone.

Convexity, which expresses the relative altitudinal difference between the focal cell and its surrounding neighbors, does not seem to affect species richness. Significantly positive associations between species richness and slope were found at fine and coarse scales. The number of species increases with increasing terrain steepness, but only at very close range, which means that the increasing richness is found at the transitions from the hill bottom (or the plateau) to the adjacent slope. This is plausible, but we are unable to provide an explanation for the significant association at the 50 m scale.

The association between species richness and

aspect (east has low values, west has high values) is negative and highly significant at fine scales. This means that the number of species is increasing when the aspect changes at close range from west to east.

#### 3.2 Habitat Types and Indicator Species

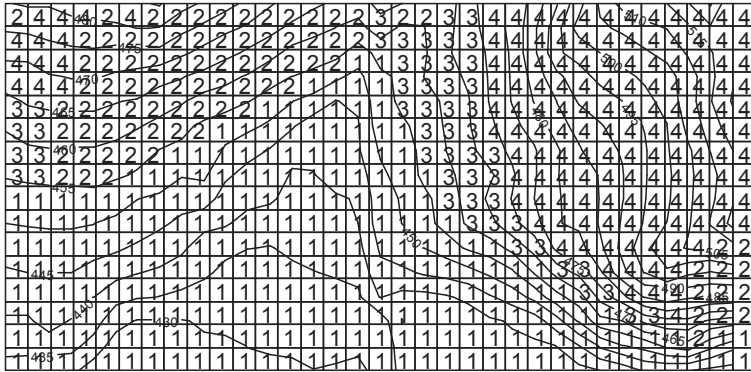
The experimental area was subdivided into four habitat types using a MRT method. The tree size was selected using a cross-validation procedure, with the four-leaf tree clearly identified as having the smallest cross-validated relative error (CV error=0.635; see Appendix 4). The geographical profile of the four habitat types is shown (Fig. 2). Each 20 m×20 m cell is assigned to one specific habitat, as indicated by the numbers 1, 2, 3 and 4.

The topographic attributes of the four habitat types are presented in Table 2. Habitat type 1, which occurs in 248 cells, occupies the low-altitudes. It is separated from habitat type 2, 3 and 4 by the lower altitudinal boundary of 453.6 m. Habitat type 2 (n=85) occupies the east-facing cells with aspects less than 187°, in the lower right and upper left of the plot. Habitat type 3 (n=52) and habitat type 4 (n=143) are found in the westward-facing cells with aspects exceeding 187°, in the upper right and upper left of the plot. Habitat type 3 occupies altitudes below, habitat type 4 altitudes above 465.7 m.

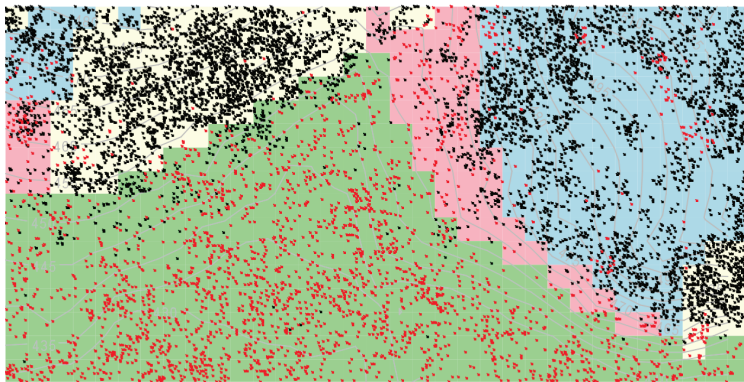
According to the MRT analysis, 38 of the 47 species occurring in the experimental area, were found to be significant indicators of the habitat types. Fifteen of these, listed in Appendix 5, are significant indicators of habitat type 1, five of habitat type 2, seven of habitat type 3, and eleven of habitat type 4.

**Table 1.** Correlation coefficients showing the degree of correlation between species richness and four topographic variables at six different spatial scales

Scales	Altitude	Convexity	Slope	Aspect
5 m×5 m	-0.1263***	0.0056	0.0332**	-0.0453***
10 m×10 m	-0.2537***	-0.0163	-0.0084	-0.0690*
20 m×20 m	-0.2896***	-0.0934*	-0.0055	-0.0542
30 m×30 m	-0.1767**	-0.0596	0.0290	0.0715
40 m×40 m	-0.1341	-0.2208*	0.1966*	0.1483
50 m×50 m	0.0565	-0.1869	0.3020**	0.2518*



**Fig. 2.** Map showing the distribution of the four habitat types at the 20 m × 20 m scale. The lines show the elevation contours at 5 m intervals.



**Fig. 3.** Map showing the spatial distribution of two species with distinct habitat preference: *Ulmus davidiana* var. *japonica* (red dots) and *Carpinus cordata* (black dots). Background colors: green = habitat type 1; yellow = habitat type 2; red = habitat type 3; blue = habitat type 4.

**Table 2.** Topographic attributes of the four habitat types.

Habitat types	Elevation			Convexity			Slope			Aspect		
	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
Habitat 1	426.3	439.9	453.5	-6.6	-0.5	1.5	1.4	10.3	38.3	41.9	187.5	329.7
Habitat 2	453.7	466.6	501.2	-2.9	0.5	4.3	5.3	15.7	39.2	140.5	164.1	185.9
Habitat 3	454.0	459.6	465.7	-1.4	0.0	2.9	5.5	13.5	33.1	188.9	231.2	275.7
Habitat 4	465.7	489.4	519.7	-1.1	0.6	4.7	3.9	15.9	37.3	187.6	239.9	286.3

Some species show distinct habitat-dependence, which becomes apparent when their spatial distributions are mapped. An example involving two species *Ulmus davidiana* var. *japonica* and *Carpinus cordata*, each of which has a distinct

habitat preference, is presented (Fig. 3). *Ulmus davidiana* var. *japonica* correlates negatively with the elevation, the slope, and the convexity. *Carpinus cordata*, on the other hand, correlates positively with the elevation, the slope, the convexity

**Table 3.** Significant habitat associations, based on three methods: randomized habitats, randomized species and PCM. The symbol “+” represents significant positive, “-” significant negative associations.

Habitat association	Randomized habitats	Randomized species	PCM
Habitat 1 +	16	21	16
Habitat 2 +	2	10	4
Habitat 3 +	0	13	5
Habitat 4 +	24	20	10
Total positive	42	64	35
Habitat 1 -	18	21	1
Habitat 2 -	24	27	1
Habitat 3 -	25	7	0
Habitat 4 -	5	20	0
Total negative	72	75	2
Grand Total	114	139	37

and the aspect. Both correlations are significant. This explains the different species-habitat associations of the two species and their distribution in the experimental area.

### 3.3 Species-Habitat Associations

Altogether 47 tree and shrub species, accounting for 99.7% of all individuals, were available to identify possible species-habitat associations within the research plot. Out of 188 potential species-habitat associations (four habitat types × 47

species), 114 were significantly positive or negative based on the habitat randomization procedure. The randomized-species model reveals 139 significant associations, whereas the PCM only shows 37 associations which are significant. The PCM process identifies comparatively few associations, but is much more realistic than the randomized-species and habitat randomization processes which do not consider the spatial auto-correlation of species and habitat, respectively.

Based on the PCM model, 34 out of 47 species were significantly associated with one or more habitat types, only two of these were negative. The habitat randomization produced 39, the species randomization all 47 species with significant associations (Table 3; see also Appendix 6, 7 and 8). These associations were positive as well as negative. Again, habitat randomization and the randomized-species approach produced an inflated number of significant associations. The PCM model appears to give more realistic results.

Table 4 shows four cross tabulations with the numbers of common species-habitat associations, based on the PCM model. Few species are significantly associated with more than one habitat. Most habitat pairs have zero common species-habitat associations which are either significantly positive or negative. Significant associations across several habitat types are very rare.

**Table 4.** Cross tabulations of common species-habitat associations based on the PCM. The symbol “+” indicates significant positive, “-” significant negative associations; N indicates no significant associations.

	Habitat 2+	Habitat 2N	Habitat 2-		Habitat 3+	Habitat 3N	Habitat 3-
Habitat 1+	0	16	0	Habitat 2+	1	4	0
Habitat 1N	4	26	1	Habitat 2N	4	38	0
Habitat 1-	1	0	0	Habitat 2-	1	0	0
	Habitat 3+	Habitat 3N	Habitat 3-		Habitat 4+	Habitat 4N	Habitat 4-
Habitat 1+	0	16	0	Habitat 2+	1	3	0
Habitat 1N	5	25	0	Habitat 2N	9	33	0
Habitat 1-	0	1	0	Habitat 2-	0	1	0
	Habitat 4+	Habitat 4N	Habitat 4-		Habitat 4+	Habitat 4N	Habitat 4-
Habitat 1+	0	16	0	Habitat 3+	0	5	0
Habitat 1N	10	20	0	Habitat 3N	10	32	0
Habitat 1-	0	1	0	Habitat 3-	0	0	0



## 4 Discussion

Habitat specialization is a prominent topic used to explain particular patterns of species coexistence in a forest community. Several studies in tropical forests could identify some species-habitat associations, but similar investigations seem to be lacking for temperate forest ecosystems. Accordingly, the purpose of this study is to broaden our understanding of the structuring forces in a temperate multi-species forest ecosystem with particular reference to species-habitat associations based on topographic features.

We found that spatial autocorrelation of species and topographic variables may confuse the contribution of topographic variation to plant spatial patterns. The spatial distributions of most of the tree and shrub species in our experimental plot were distinctly aggregated. Species autocorrelation may be the result of seed-dispersal limitations of most tree species. For this reason, it was necessary to reduce the effects of autocorrelation, regarding species as well as habitat.

### 4.1 Habitat Types and Indicator Species

The experimental plot was subdivided into four habitat types sharing topographic characteristics. Habitat type 1 has the largest area and occupies the low altitudes. Almost half of all the significant species-habitat associations were identified in habitat type 1, when considering both habitat and species autocorrelation.

The lower plateau is characterized by moist and wet soil conditions. The cells on the lower plateau and lower gentle slopes (habitat types 1 and 3) have two types of indicators: light and moisture-demanding pioneer and shade tolerant understorey species, including *Betula* spp., *Euonymus* spp., *Acer* spp., *Malus baccata* (L.) Borkh. and *Syringa reticulata* var. *amurensis*. The high lying areas and steep slopes (habitat types 2 and 4) are characterized by well-drained soil conditions. These habitat types have more climax indicator species, such as *Pinus koraiensis*, *Acer mono*, *Tilia amurensis*, and *Quercus mongolicus* Fisch. Some harvesting has taken place in the experimental area during the early 1960's, but details are not available.

Based on the results obtained with the PCM model, the percentage of species showing significant associations with habitat type 1 (45.9%) and habitat type 4 (27.0%) is consistent with the relative habitat areas in the two dominant habitat types. Habitat type 1 occupies 47 per cent of the total experimental area, habitat type 4 only 27 per cent. This almost exact match is likely to be accidental. However, the bigger areas naturally support a greater number of species which are candidates for significant species-habitat associations. Habitat types 2 and 3 represent the transitional zones between the low and high plateau. Again, the total percentage of habitat-associated species in both types together (27.0%) closely matches that of their total area (25.9%). Thus, the number of habitat-associated species in a specific habitat may depend on the available habitat area. This is a species-area phenomenon. Due to the increasing number of trees, more habitat specialists can be found in habitat types that occupy larger areas. This is simply an effect of the species-area relationship. However, this effect does not contradict the occurrence of species specialization. The majority of the species in our experimental area showed significant positive or negative associations with specific habitat types.

The complex topography in the study area includes habitat types which are preferred by different tree and shrub species, resulting in a high proportion of distinct species-habitat associations. Our indicator species analysis showed that 38 out of 47 of the more common species were indicative of specific habitat types. The indicative power was rather variable among the different indicator species. For example, in habitat type 1, *Ulmus davidiana* var. *japonica* showed the highest indicator value (0.62), while *Betula platyphylla* Suk. had the lowest indicator value (0.10).

### 4.2 Species-Habitat Associations

Almost all the studies about species-habitat associations, based on data from large experimental areas, were conducted in tropical or subtropical forest ecosystems. Harms et al. (2001) identified six habitat types in the tropical forest in *Barro Colorado Island*, where many species had strong species-habitat associations. Similar results were

obtained in other tropical forests (Harms et al. 2001, Itoh et al. 2003, Russo et al. 2005, Yamada et al. 2006, 2007, John et al. 2007). Our study appears to be among the first ones based on data from a large experimental area in a temperate forest ecosystem.

Altogether 34 species (72.3% of the total number) are associated with at least one habitat type, based on the conservative PCM model. Interestingly, these 34 species only produce 35 significantly positive species-habitat associations (out of 136 potential associations). Almost each of these species shows a unique positive association with a particular habitat. *Ulmus davidiana* var. *japonica* is an exception, being significantly associated with two habitat types simultaneously. The patterns of different species specializing in the different habitat types can be interpreted by the life history strategies (for example, shade tolerance, growth and mortality rates, etc). According to Nakashizuka et al. (1992) and Masaki et al. (1999), shade-tolerant species have recruitment rates that are almost equivalent to, or significantly larger than mortality rates. This means that their populations can be maintained or may even increase under natural conditions. Understory shade-tolerant species, such as *Lonicera ruprechtiana* Regel., *Rhamnus davurica* Pall., *Euonymus macropterus* Rupr., *Viburnum sargentii* Koehne, are neutrally associated with all four habitat types in the research plot. Some dominant canopy species, such as *Tilia amurensis*, *Pinus koraiensis*, *Acer mono* and *Ulmus spp.* show a strong adaptability toward habitat variations. These species did not indicate any particular habitat preference and had neutral associations with all habitat types.

Species may differ from each other in their habitat preference. They are presumed to be capable of locating themselves in different positions along habitat gradients. For example, *Fraxinus mandshurica* specializes on habitat type 1, while *Quercus mongolica* clearly prefers habitat type 4. This corresponds to the ecological characteristics of the two species. *Fraxinus mandshurica* prefers fertile, moist and well drained sites, and usually occurs on the gentle slopes. The cells of habitat type 1 are located on these sites. *Quercus mongolica* prefers dry sites, and is usually found on the hilltop and lower ridges. That is where the cells of habitat type 4 are found.

The distribution of some species reflects regeneration following local disturbance. *Betula platyphylla*, for example, is a light-demanding and shade-intolerant tree species. The species is positively associated with habitat type 1 where heavy cutting disturbance occurred about 50 years ago. *Viburnum burejaeticum* Regel et Herd which is a distinctly light-demanding species, showed a particular preference for habitat type 3 and a negative association with habitat type 2. These habitat types differ with regard to aspect. The cells in habitat type 3 are located on sunny south-facing slopes, while most cells in habitat type 2 are found on rather more shaded south-westerly slopes.

Habitat differentiation and spatial limitations due to species dispersal are two key factors that contribute to structuring forest communities. The habitat differentiation theory is based on the idea that there is a trade-off between growth/survival rates and resource availability (Kitajima 1994, Wright et al. 2003), producing environmentally dependent species preferences. This theory seems to represent the existing mainstream view (Clark et al. 1999, Svenning 2004, Harms et al. 2001, Wright 2002). Several studies have shown that forest community structure is governed by seed dispersal limitation and demographic stochasticity (Hubbell et al. 1999, Bell 2001, Hubbell 2001). These findings are supported by evidence of seed dispersal limitation (Hubbell et al. 1999, Dalling et al. 2002) and nonenvironmental spatial dependency in species distributions (Svenning 2001, Tuomisto et al. 2003).

The understanding of species-habitat associations depends largely on the ability to reduce the effects of autocorrelation, regarding species as well as habitat. Spatial autocorrelation cannot be ignored when considering species-habitat associations (Legendre and Legendre 1998). Restricted seed dispersal and autocorrelated habitat types may create an artificially inflated effect to species-habitat associations. This study has shown that randomizing species (under the CSR model) and randomizing habitat types seriously overestimate the number of distinct habitat associations. For this reason, the more realistic and conservative PCM model was also used. The PCM approach identified much less significant species-habitat associations (only 37, see Table 3) than the species and habitat randomization methods (114 and

139 significant associations, respectively). Our results indicate that habitat differentiation and dispersal limitation are not mutually exclusive. Both contributed simultaneously to the maintenance of the particular distribution of the tree and shrub species in our experimental area.

A species which is positively associated with a particular habitat can be expected to have a greater competitive advantage than other species that are neutrally or negatively associated with the same habitat. According to an earlier result presented by Harms et al. (2001) in a tropical forest, if negative associations were used to identify disappearing (“sink”) subpopulations within the research area, then the list of species neutrally or positively associated with a particular habitat type would be equal to the number capable of sustaining populations if the plot was composed of only that habitat type. According to our PCM tests, 32 out of 47 species were neutrally or positively associated with the four habitat types. Habitat types 1 and 2 were negatively associated (avoided) by *Acer tegmentosum* Maxim. and *Viburnum burejaeticum* respectively, based on the PCM model. This leaves 46 species which are neutrally or positively associated with either habitat type 1 or 2. No negative species-habitat associations were found in habitat type 3 and 4.

Habitat types are not closed systems, and there are immigrations between them via seed dispersals on short- and/or long-distances. This suggests that species assemblages will be influenced significantly by species input from the surrounding habitat types. Thus, the high proportion of species in these assemblages might be maintained by persistent immigration, not by habitat differentiation among coexisting species. Sink areas are subsidized by sources and even strong habitat preference of trees and shrubs does not seem to provide sufficient support for the hypothesis that habitat differentiation maintains high species diversity.

Future studies of species-habitat associations should therefore examine whether habitat, if not subsidized by immigration, would be able to support non-negative tree population growth.

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*Total of 36 references*

**Appendix 1.** The total basal area of dominant tree species in research plot.

Tree species	Total basal area (m <sup>2</sup> /ha)
<i>Ulmus davidiana</i> var. <i>japonica</i>	0.4309
<i>Pinus koraiensis</i>	0.6833
<i>Juglans mandshurica</i>	1.8705
<i>Tilia mandschurica</i>	0.6098
<i>Carpinus cordata</i>	0.3813
<i>Acer mono</i>	1.2182
<i>Fraxinus mandshurica</i>	0.6023
<i>Tilia amurense</i>	0.8771
<i>Ulmus laciniata</i>	0.9912

**Appendix 2.** Stem density of the top five species in research plot.

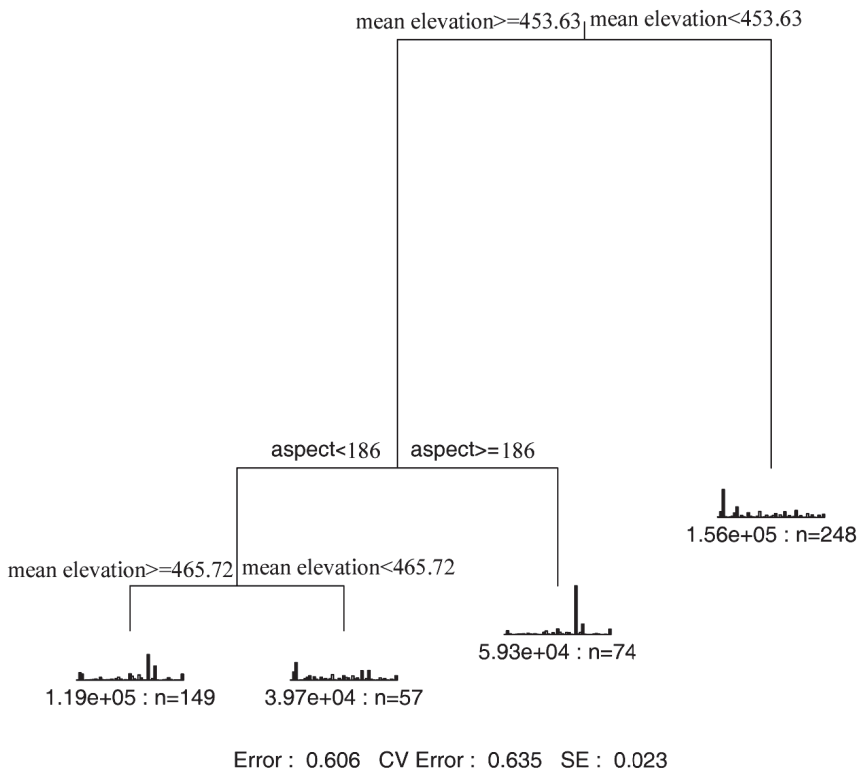
Tree species	Stem density (stems/ha)
<i>Acer mandshuricum</i>	150
<i>Syringa reticulata</i> var. <i>amurensis</i>	412
<i>Ulmus davidiana</i> var. <i>japonica</i>	141
<i>Carpinus cordata</i>	393
<i>Acer mono</i>	240

**Appendix 3.** List of the 47 species used in the analysis

Species*	Family	Life forms
<i>Betula platyphylla</i>	Betulaceae	Tree
<i>Acer mandshuricum</i>	Aceraceae	Tree
<i>Syringa reticulata</i> var. <i>amurensis</i>	Oleaceae	Small tree/tree
<i>Acer ginnala</i>	Aceraceae	Shrub/small tree
<i>Lonicera ruprechtiana</i>	Caprifoliaceae	Shrub
<i>Rhamnus davurica</i>	Rhamnaceae	Shrub/small tree
<i>Euonymus macropterus</i>	Celastraceae	Shrub
<i>Padus racemosa</i>	Rosaceae	Tree
<i>Ulmus davidiana</i> var. <i>japonica</i>	Ulmaceae	Tree
<i>Acanthopanax senticosus</i>	Araliaceae	Shrub
<i>Acer barbinerve</i>	Aceraceae	Small tree
<i>Ulmus macrocarpa</i>	Ulmaceae	Shrub/tree
<i>Berberis amurensis</i>	Berberidaceae	Shrub
<i>Lonicera maaackii</i>	Caprifoliaceae	Shrub
<i>Philadelphus schrenkii</i>	Saxifragaceae	Shrub
<i>Rhamnus schneideri</i> var. <i>manshurica</i>	Rhamnaceae	Shrub
<i>Betula costata</i>	Betulaceae	Tree
<i>Pinus koraiensis</i>	Pinaceae	Tree
<i>Juglans mandshurica</i>	Juglandaceae	Tree
<i>Fraxinus rhynchophylla</i>	Oleaceae	Tree
<i>Maackia amurensis</i>	Leguminosae	Tree
<i>Phellodendron amurense</i>	Rutaceae	Tree
<i>Viburnum sargentii</i>	Caprifoliaceae	Shrub
<i>Tilia mandshurica</i>	Tiliaceae	Tree
<i>Ulmus laciniata</i>	Ulmaceae	Tree
<i>Euonymus verrucosus</i>	Celastraceae	Shrub
<i>Aralia elata</i>	Araliaceae	Shrub
<i>Corylus mandshurica</i>	Betulaceae	Shrub
<i>Quercus mongolica</i>	Fagaceae	Tree
<i>Acer triflorum</i>	Aceraceae	Tree
<i>Viburnum burejaeticum</i>	Caprifoliaceae	Shrub
<i>Carpinus cordata</i>	Betulaceae	Tree
<i>Acer tegmentosum</i>	Aceraceae	Tree
<i>Actinidia arguta</i>	Actinidiaceae	Liana
<i>Acer mono</i>	Aceraceae	Tree
<i>Abies holophylla</i>	Pinaceae	Tree
<i>Malus baccata</i>	Rosaceae	Tree
<i>Pyrus ussuriensis</i>	Rosaceae	Tree
<i>Populus davidiana</i>	Salicaceae	Tree
<i>Fraxinus mandshurica</i>	Oleaceae	Tree
<i>sorbus alnifolia</i>	Rosaceae	Tree
<i>Euonymus alatus</i>	Celastraceae	Shrub
<i>Rhamnus ussuriensis</i>	Rhamnaceae	Shrub
<i>Rhamnus parvifolia</i>	Rhamnaceae	Shrub
<i>Rhamnus diamantiaca</i>	Rhamnaceae	Shrub
<i>Lonicera praeflorens</i>	Caprifoliaceae	Shrub
<i>Tilia amurensis</i>	Tiliaceae	Tree

\* The species were identified using the records in the Chinese Virtual Herbarium (see <http://www.cvh.org.cn/cms/>)

**Appendix 4.** Multivariate regression tree for the species composition data. Euclidean distance was used for splitting. Barplots show the multivariate species mean at each node, and the numbers of sites are shown in parentheses.



**Appendix 5.** Results of indicator species analysis.

Species	Habitat type	Indicator value	Probability
<i>Ulmus davidiana</i> var. <i>japonica</i>	Habitat 1	0.6178	0.001
<i>Acer triflorum</i>	Habitat 1	0.6054	0.001
<i>Syringa reticulata</i> var. <i>mandshurica</i>	Habitat 1	0.5329	0.001
<i>Lonicera maackii</i>	Habitat 1	0.4643	0.001
<i>Malus baccata</i>	Habitat 1	0.4508	0.001
<i>Fraxinus mandshurica</i>	Habitat 1	0.3961	0.001
<i>Rhamnus davurica</i>	Habitat 1	0.3574	0.001
<i>Padus racemosa</i>	Habitat 1	0.353	0.001
<i>Juglans mandshurica</i>	Habitat 1	0.3134	0.001
<i>Euonymus macropterus</i>	Habitat 1	0.2823	0.001
<i>Euonymus alatus</i>	Habitat 1	0.2693	0.001
<i>Phellodendron amurense</i>	Habitat 1	0.2429	0.006
<i>Acer ginnala</i>	Habitat 1	0.1157	0.001
<i>Maackia amurensis</i>	Habitat 1	0.1147	0.001
<i>Betula platyphylla</i>	Habitat 1	0.1007	0.023
<i>Carpinus cordata</i>	Habitat 2	0.5743	0.001
<i>Pinus koraiensis</i>	Habitat 2	0.2395	0.01
<i>Actinidia arguta</i>	Habitat 2	0.2172	0.001
<i>Acer tegmentosum</i>	Habitat 2	0.1769	0.001
<i>Aralia elata</i>	Habitat 2	0.0403	0.026
<i>Acer mandshuricum</i>	Habitat 3	0.2847	0.016
<i>Philadelphus schrenkii</i>	Habitat 3	0.2149	0.002
<i>Acer barbinerve</i>	Habitat 3	0.1892	0.033
<i>Abies holophylla</i>	Habitat 3	0.1184	0.005
<i>Rhamnus schneideri</i> var. <i>manshurica</i>	Habitat 3	0.117	0.014
<i>Euonymus macropterus</i>	Habitat 3	0.1117	0.047
<i>Betula costata</i>	Habitat 3	0.0961	0.002
<i>Acer mono</i>	Habitat 4	0.3386	0.003
<i>Sorbus alnifolia</i>	Habitat 4	0.3122	0.001
<i>Ulmus laciniata</i>	Habitat 4	0.31	0.001
<i>Tilia mandshurica</i>	Habitat 4	0.2752	0.001
<i>Tilia amurensis</i>	Habitat 4	0.2721	0.025
<i>Corylus mandshurica</i>	Habitat 4	0.2457	0.008
<i>Fraxinus rhynchophylla</i>	Habitat 4	0.2106	0.001
<i>Quercus mongolica</i>	Habitat 4	0.1983	0.026
<i>Rhamnus parvifolia</i>	Habitat 4	0.0663	0.004
<i>Lonicera praeflorens</i>	Habitat 4	0.0641	0.032
<i>Acanthopanax senticosus</i>	Habitat 4	0.0453	0.05



**Appendix 6.** Species-habitat associations using the PCM model. “p” and “n” denote to “positive” and “negative”, respectively. \*, \*\* and \*\*\* indicate significance at  $p < 0.05$ , 0.01 and 0.001, respectively.

Species	Habitat 1	Habitat 2	Habitat 3	Habitat 4
<i>Betula platyphylla</i>	p*			
<i>Acer mandshuricum</i>				
<i>Syringa reticulata</i> var. <i>amurensis</i>	p***			
<i>Acer ginnala</i>	p***			
<i>Lonicera ruprechtiana</i>				
<i>Rhamnus davurica</i>				
<i>Euonymus macropterus</i>				
<i>Padus racemosa</i>	p***			
<i>Ulmus davidiana</i> var. <i>japonica</i>	p***			
<i>Acanthopanax senticosus</i>				p**
<i>Acer barbinerve</i>				
<i>Ulmus macrocarpa</i>				
<i>Berberis amurensis</i>		p***		
<i>Lonicera maackii</i>	p***			
<i>Philadelphus schrenkii</i>	p*			
<i>Rhamnus schneideri</i> var. <i>manshurica</i>			p*	
<i>Betula costata</i>			p***	
<i>Pinus koraiensis</i>				
<i>Juglans mandshurica</i>	p***			
<i>Fraxinus rhynchophylla</i>				p***
<i>Maackia amurensis</i>	p***			
<i>Phellodendron amurense</i>	p*			
<i>Viburnum sargentii</i>				
<i>Tilia mandshurica</i>				p**
<i>Ulmus laciniata</i>				
<i>Euonymus verrucosus</i>	p*			
<i>Aralia elata</i>		p*		
<i>Corylus mandshurica</i>				p**
<i>Quercus mongolica</i>				p*
<i>Acer triflorum</i>	p***			
<i>Viburnum burejaeticum</i>			p***	
<i>Carpinus cordata</i>		n***		p*
<i>Acer tegmentosum</i>	n**	p***		
<i>Actinidia arguta</i>		p***		
<i>Acer mono</i>				
<i>Abies holophylla</i>			p*	
<i>Malus baccata</i>	p***			
<i>Pyrus ussuriensis</i>				
<i>Populus davidiana</i>				p*
<i>Fraxinus mandshurica</i>	p***			
<i>Sorbus alnifolia</i>				p**
<i>Euonymus alatus</i>	p***			
<i>Rhamnus ussuriensis</i>			p*	
<i>Rhamnus parvifolia</i>				p***
<i>Rhamnus diamantiaca</i>	p***			
<i>Lonicera praeflorens</i>				p***
<i>Tilia amurensis</i>				

**Appendix 7.** Species-habitat associations using the CRS model. “p” and “n” denote to “positive” and “negative”, respectively. \*, \*\* and \*\*\* indicate significance at  $p < 0.05$ , 0.01 and 0.001, respectively.

Species	Habitat 1	Habitat 2	Habitat 3	Habitat 4
<i>Betula platyphylla</i>	p***	n**		n***
<i>Acer mandshuricum</i>	n***	n***	p***	p***
<i>Syringa reticulata</i> var. <i>amurensis</i>	p***	n***		n***
<i>Acer ginnala</i>	p***	n***	n***	n***
<i>Lonicera ruprechtiana</i>		n***		
<i>Rhamnus davurica</i>	p***			n***
<i>Euonymus macropterus</i>	p***	n***	p***	n***
<i>Padus racemosa</i>	p***	n***		n***
<i>Ulmus davidiana</i> var. <i>japonica</i>	p***	n***	n***	n***
<i>Acanthopanax senticosus</i>	n*			p***
<i>Acer barbinerve</i>	n***	n***	p***	p***
<i>Ulmus macrocarpa</i>	p*	n*	p***	n**
<i>Berberis amurensis</i>	n***	p***		
<i>Lonicera maaeckii</i>	p***	n***		n***
<i>Philadelphus schrenkii</i>	p***	n***	p**	
<i>Rhamnus schneideri</i> var. <i>manshurica</i>	n***	n***	p***	p***
<i>Betula costata</i>			p***	
<i>Pinus koraiensis</i>	n***	p***		p**
<i>Juglans mandshurica</i>	p***	n***	p*	n***
<i>Fraxinus rhynchophylla</i>	n***			p***
<i>Maackia amurensis</i>	p***	n***	n***	n***
<i>Phellodendron amurense</i>	p***			n***
<i>Viburnum sargentii</i>	n***	p***	p***	p***
<i>Tilia mandshurica</i>	n***	n*		p***
<i>Ulmus laciniata</i>	n***	n*		p***
<i>Euonymus verrucosus</i>	p***	n***		n***
<i>Aralia elata</i>	n***	p***		p*
<i>Corylus mandshurica</i>	n***	n***	p***	p***
<i>Quercus mongolica</i>	n***	p***		p***
<i>Acer triflorum</i>	p***	n***	n***	n***
<i>Viburnum burejaeticum</i>	p***	n***		n*
<i>Carpinus cordata</i>	n***	p***	n***	p***
<i>Acer tegmentosum</i>	n***	p***		
<i>Actinidia arguta</i>	n***	p***	p*	p***
<i>Acer mono</i>	n***	p***		p***
<i>Abies holophylla</i>		n*	p***	n***
<i>Malus baccata</i>	p***	n***	n***	n***
<i>Pyrus ussuriensis</i>	p**			
<i>Populus davidiana</i>	n***			p***
<i>Fraxinus mandshurica</i>	p***	n***		n***
<i>Sorbus alnifolia</i>	n***			p***
<i>Euonymus alatus</i>	p***	n***		n***
<i>Rhamnus ussuriensis</i>			p***	
<i>Rhamnus parvifolia</i>	n***	n***	n*	p***
<i>Rhamnus diamantiaca</i>	p***	n***		n***
<i>Lonicera praeflorens</i>	n***			p***
<i>Tilia amurensis</i>		p***		p***

**Appendix 8.** Species-habitat associations based on habitat randomization. “p” and “n” denote to “positive” and “negative”, respectively. \*, \*\* and \*\*\* indicate significance at  $p < 0.05$ , 0.01 and 0.001, respectively.

Species	Habitat 1	Habitat 2	Habitat 3	Habitat 4
<i>Betula platyphylla</i>	p***	n**	n**	
<i>Acer mandshuricum</i>		n***	n***	p***
<i>Syringa reticulata</i> var. <i>amurensis</i>	p***	n***	n***	
<i>Acer ginnala</i>	p***	n**	n**	
<i>Lonicera ruprechtiana</i>		n*		p*
<i>Rhamnus davurica</i>				
<i>Euonymus macropterus</i>				
<i>Padus racemosa</i>	p***	n***	n**	
<i>Ulmus davidiana</i> var. <i>japonica</i>	p***	n***	n***	n***
<i>Acanthopanax senticosus</i>				p***
<i>Acer barbinerve</i>		n***		p***
<i>Ulmus macrocarpa</i>				
<i>Berberis amurensis</i>	n*			p*
<i>Lonicera maackii</i>	p***	n***	n***	n***
<i>Philadelphus schrenkii</i>	p***	n***		p*
<i>Rhamnus schneideri</i> var. <i>manshurica</i>	n**	n***		p***
<i>Betula costata</i>				
<i>Pinus koraiensis</i>	n***		n***	p***
<i>Juglans mandshurica</i>		n***	n***	p***
<i>Fraxinus rhynchophylla</i>	n***		n**	p***
<i>Maackia amurensis</i>	p***	n***	n***	
<i>Phellodendron amurense</i>	p***		n***	
<i>Viburnum sargentii</i>				
<i>Tilia mandshurica</i>	n***		n**	p***
<i>Ulmus laciniata</i>	n***	n***	n***	p***
<i>Euonymus verrucosus</i>	p***	n***	n***	
<i>Aralia elata</i>	n**			p**
<i>Corylus mandshurica</i>	n***	n***		p***
<i>Quercus mongolica</i>	n***		n***	p***
<i>Acer triflorum</i>	p***	n***	n***	n***
<i>Viburnum burejaeticum</i>	p*	n***		
<i>Carpinus cordata</i>	n***	p***	n***	p***
<i>Acer tegmentosum</i>	n***	p**		p**
<i>Actinidia arguta</i>	n***		n**	p***
<i>Acer mono</i>	n***	n*	n***	p***
<i>Abies holophylla</i>				
<i>Malus baccata</i>	p***	n***	n***	n***
<i>Pyrus ussuriensis</i>				
<i>Populus davidiana</i>	n***			p***
<i>Fraxinus mandshurica</i>	p***	n***	n***	
<i>Sorbus alnifolia</i>	n***	n***	n***	p***
<i>Euonymus alatus</i>	p***	n***	n***	
<i>Rhamnus ussuriensis</i>				
<i>Rhamnus parvifolia</i>	n**			p***
<i>Rhamnus diamantiaca</i>	p***	n***	n***	n**
<i>Lonicera praeflorens</i>	n***			p***
<i>Tilia amurensis</i>	n***			p***