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RESEARCH ARTICLE

Habitat associations of saplings and adults in an old-growth temperate forest in the Changbai mountains, northeastern China

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Abstract Species-habitat association analysis is useful to detect spatial arrangement of individual plants, to discover rules about the distribution of species and to generate hypotheses about the possible underlying process controlling observed structures. Quantifying methods were used to classify habitats in terms of topographical variables in a mixed temperate broad-leaved Korean pine forest of the Changbai mountains in northeastern China. All of the 625 20 m × 20 m quadrats of the plot could be unambiguously assigned to one of three habitat categories (low-plateau, high-plateau and slope). Torus-translation tests were used to estimate species-habitat associations. Many species are clearly distributed in a biased fashion with respect to habitats. Fifteen (55.6%) out of 27 species showed strong positive or negative association with specific habitats. We compared species-habitat associations at the sapling and adult stages. Adjusted density values indicated few species exhibit extremely strong habitat associations. Only 9 out of 26 species had adjusted densities > 3 in the habitat for which they had strong positive affinity. Few species show the same associations at the small tree and large tree stages. Only 3 out of 22 occurring associations with a specific habitat appeared to have a consistent habitat association at the two stages. These results suggest that species-habitat associations exist in the 25-ha plot of the temperate forest of the Changbai mountains. Owing to limitations in our statistical methodology, we partly underestimated associations by ignoring rare species. Regeneration niches can contribute to co-existence, but regeneration niches due to habitat associations play a limited role in species co-existence, since most species show a similar trend in habitat associations at the sapling and adult stages. We should pay more attention to shifts in habitat associations, i.e. niche shifts at different stages of existence.

Key words niche differentiation, habitat association, environmental heterogeneity, saplings and adults, life stages

1 Introduction

Niche differentiation concerning resources was a notable hypothesis in trying to explain the maintenance of tree species diversity (Leigh, 1999). Species-habitat associations are the most direct way to test the contributions about niche differentiation to species coexistence (Tilman and Pacala, 1993). Some theoretical models had predicted species coexistence in heterogeneous environments where each species was best suited to a particular habitat (Tilman and Pacala, 1993). Recent studies have widely documented local-scale associations between tree species and habitat types in tropical forests. Many tree species were found to be significantly associated, either positively or negatively, with slopes, swamps and low-lying plateaux in lowland tropical forests (Hubbell and Foster, 1986; Svenning, 1999, 2001b; Harms et al., 2001; Aiba et DO .XHRYiDQG KWU 9DOHQFLDHWDO 2004; DeWalt et al., 2006), as well as with aspect, elevation and particular local conditions, such as gaps or dry soils in mountain forests (Svenning, 2001a). These studies mainly concentrated on the tropical Forest Dynamics Project (FDP) plots, such as the Barro Colorado Island (BCI) (Harms et al., 2001) or the Sinharaja Plots (Gunatilleke et al., 2006). Similar studies on species-habitat associations were less prevalent for temperate forests due to a lack of large forest plots. Topography was the most important habitat factor that affected spatial variability of climate, soil prop-

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erties and species distribution. Habitat topography usually was defined by subjective judgment in the survey processes that were macro-scale approaches, which would also have affected the results of species habitat associations (Yamada and Suzuki, 1997; Svenning, 1999). The definition of habitat topography was always somewhat arbitrary, making comparisons between studies by different authors difficult. As a consequence, some quantitative methods were developed to classify habitat types in terms of topographical variables (Harms et al., 2001; Valencia et al., 2004).

Chi-square test was a common method for testing species-habitat associations in earlier studies (Hubbell and Foster, 1983, 1986; Clark et al., 1998). The test required that the sampling units be independent. However, most tree species displayed patterns of patchy distribution (Condit et al., 2000) and the abundance of different tree species in continuously arranged sampling units were spatially autocorrelated (Roxburgh and Chesson, 1998; Webb and Peart, 2000). Spurious statistical associations between species and topography may have occurred due to coincidental similarity between spatial structures of population of species and topography, since both tree species and topography showed spatially autocorrelated patterns of distribution. This meant that the assumption of randomness was violated and thus traditional statistical tests cannot be applied (Roxburgh and Chesson, 1998; Webb and Peart, 2000). Torus-translation tests considering spatial autocorrelation were available for testing species-habitat associations. These tests are even more conservative than Chi-square tests (Harms et al., 2001). More recent studies used torus-translation tests to estimate habitat associations in recent reports on tropical forests (Harms et al., 2001; Gunatilleke et al., 2006).

Furthermore, because adults usually cannot specialize on resources, Grubb (1977) suggested that habitat partitioning occurs during early stages in the life of trees and that coexistence is possible through partitioning of regeneration niches. If niche differentiation was most likely to take place during regeneration, then observed associations with topography would be possible to arise during early life stages, such as seed germination and seedling establishment. In addition, physiological requirements and selective pressures may change with tree size, such that the ecological preferences of a species may differ from one life stage to the next (Werner and Gilliam, 1984; Schupp, 1995). However, comparisons of habitat associations of species at multiple stages are rare (Webb and Peart, 2000; Comita et al., 2007). Thus, it remains unclear from observed species-habitat associations whether such associations actually reflect regeneration niche differences.

The Changbai Mountain National Nature Reserve is located in the northeast of China and has remained an intact primary temperate forest. The mixed broad-leaved Korean pine forest within the reserve is a typical temperate forest in northeastern China and about 300 years old. According to the census measure of BCI plots, a 25-ha dynamic forest plot was established and surveyed in this mixed broad-leaved Korean pine forest in 2004. We used these data to analyze habitat associations of saplings and adults in this typical temperate forest. The objectives of this study were 1) to identify species-habitat associations in a typical temperate forest; 2) to analyze if species show similar habitat associations across different life stages and 3) to understand if there were effects of regeneration niche on species coexistence in temperate typical forest.

2 Study area and data collection

2.1 Study area

Our study site was located at 42º12′N and 128º32′E in the Changbai mountains, a national natural reserve, in northeastern China. In 1960, the Changbai Mountain Nature Reserve was established as the largest and best protected environment of all Chinese reserves, with its ecosystem largely intact. The plant communities had clear gradient distributions with increasing elevation. There were clearly defined vertical distributed prime forest ecosystems, including four types of ecosystems ranging from mixed broad-leaved Korean pine (*Pinus koraiensis*) forests at the bottom to spruce-fir (*Picea jezoensis* and *Abies nephrolepis*) forests, subalpine birch (*Betula ermanii*) forests and a tundra zone at the top (Zhao, 1980). Mixed broad-leaved Korean pine forests occur from 500 to 1100 m elevation. The elevation of our study site was about 800 m, with a brown forest soil (Cheng et al., 1981). Mean annual precipitation at this zone is 703.62 mm and mainly concentrated in the period from June−September (500.40 mm). The mean annual temperature is 2.32°C (Chi et al., 1981).

2.2 Data collection

Our forest plot was 25-ha square: 500 m × 500 m. The plot was located in a mostly flat and relatively uniform terrain. In total, 676 points of 20 m × 20 m were established within the plot. Each 20 m × 20 m quadrat was divided into sixteen 5 m × 5 m subquadrats. Large differences at each point were noted and measured.

The plant survey was based on the subquadrats. The survey method was the same as recommended for BCI plots (Condit et al., 1994; Harms et al., 2001). We surveyed all stems of at least 1-cm diameter at breast height (DBH), recorded their geographic coordinates and identified the species. The survey was carried out in 2004.

Plot diversity revealed the following information: there were 59121 live trees (DBH ≥ 1 cm), belonging to 52 species. There were clearly a few dominant species: 3 species comprised 60.6% of all trees and 14 species contained 95.6%. The remaining 38 species only comprised fewer than 5% of all trees. One species consisted of just 1 tree, while the most frequently occurring species was *Corylus mandshurica* with 15923 stems. According to Hubbell and Foster (1986a), the species whose densities were equal to or less than one tree per ha were considered rare. By this definition, there were 17 rare species, consisting of 32.7% of all species in the plot (Hao et al., 2008).

3 Methods

The generally homogeneous environment included a number of microtopographies that may affect distribution of some species. We used 20 m × 20 m quadrats because spatial autocorrelation was strongest at scales < (20 m × 20 m) (Condit et al., 2000). Quadrats were assigned to three topographic sites according to elevation and slope, i.e., high-plateau, low-plateau and slope (the topography of our plot was more homogeneous than that of the BCI plots, so we just divided our plot into three habitat types). Elevation of a quadrat was defined as the mean elevation at its four corners. Slope was calculated following Harms et al. (2001), as the single average angle from the level of the entire quadrat. We chose the 804.0 m contour to separate the high-plateau from the low-plateau, because this was the approximate median elevation of the plot. We select an angle of 7° as the criterion for distinguishing slope and plateau, again following Harms et al. (2001). The method for dividing habitats was as follows: low plateau (slope < 7°, elevation < 804.0 m), high plateau (slope < 7°, elevation ≥ 804.0 m) and slope (slope ≥ 7 °).

3.1 Torus translation test of habitat associations

We used Harms' (1997) torus-translation to test habitat associations. We restricted our analyses to the 27 most abundant species in the three focal habitats on the plot, all with ≥ 50 stems ≥ 1-cm DBH. The torus-translation included moving the true habitat map by 20-m increments in the four cardinal directions. If the relative density of a species determined from the true habitat map was more extreme than at least 97.5% of the simulated relative densities (i.e., $\alpha = 0.05$ level of significance for a two-tailed test), then it was considered to be statistically associated (either positively or negatively) with the habitat. In other words, a species was positively associated with a particular habitat when the relative density of the proportion of a simulated map was less than the relative density of the true map with a probability ≥ 0.975; a species was negatively associated when the relative density of the proportion of a simulated map was greater than the relative density of the true map with a probability ≥ 0.975 (Harms et al., 2001). We then tested habitat associations for the selected 26 most abundant species (excluding *Viburnum sargenti* due to DBH of all stems < 2 cm) by torus-translation tests in sapling and adult stages. Considering the differences between trees and shrubs, we chose the different rule to divide trees and shrubs into saplings and adults. Given their DBH, the method of dividing saplings from adults was as follows: shrub (sapling, DBH ≤ 2 cm; adult, DBH >2 cm), adult (sapling, DBH ≤ 10 cm; adult, DBH > 10 cm).

3.2 Strength of habitat associations

Torus-translation tests determined only whether species were significantly associated with a habitat. To assess the strength of the associations, we calculated the adjusted stem density of each species for each habitat type at the sapling and adult stages by dividing the density of the species in the focal habitat by the total density of the species across the entire 25-ha plot. Adjusted stem density values > 1 suggested a positive association of a species with the habitat, while values < 1 suggested that the species avoided that habitat type. We used the same 26 most abundant species as were selected in analyzing habitat associations of adults and saplings to compare the adjusted stem density.

All analyses were carried out using the software package R version 2.1.0 (R Development Core Team, 2005).

4 Results and analyses

4.1 Plot topographic characteristics

While the environment was fairly homogeneous, it included a number of micro-habitat types. The entire plot was very flat, with a maximum elevation of 809 m, a minimum elevation of 792 m, a difference of only 17 m. The southeast angle of the plot had a few

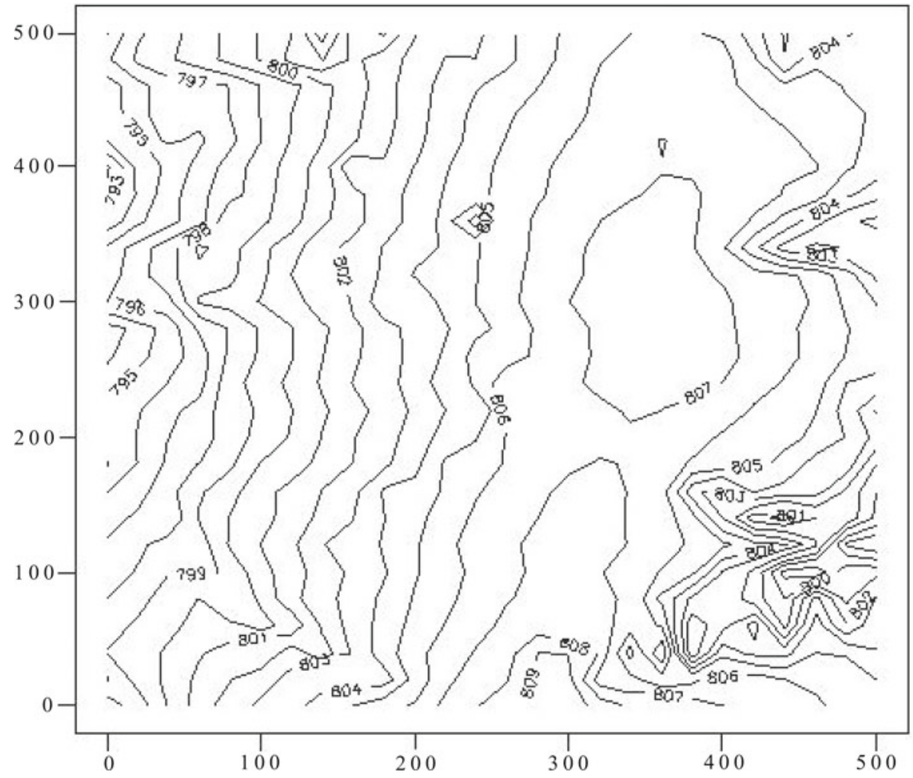

Fig. 1 Contour map of 25-ha plot based on mark points on 20 m × 20 m grid

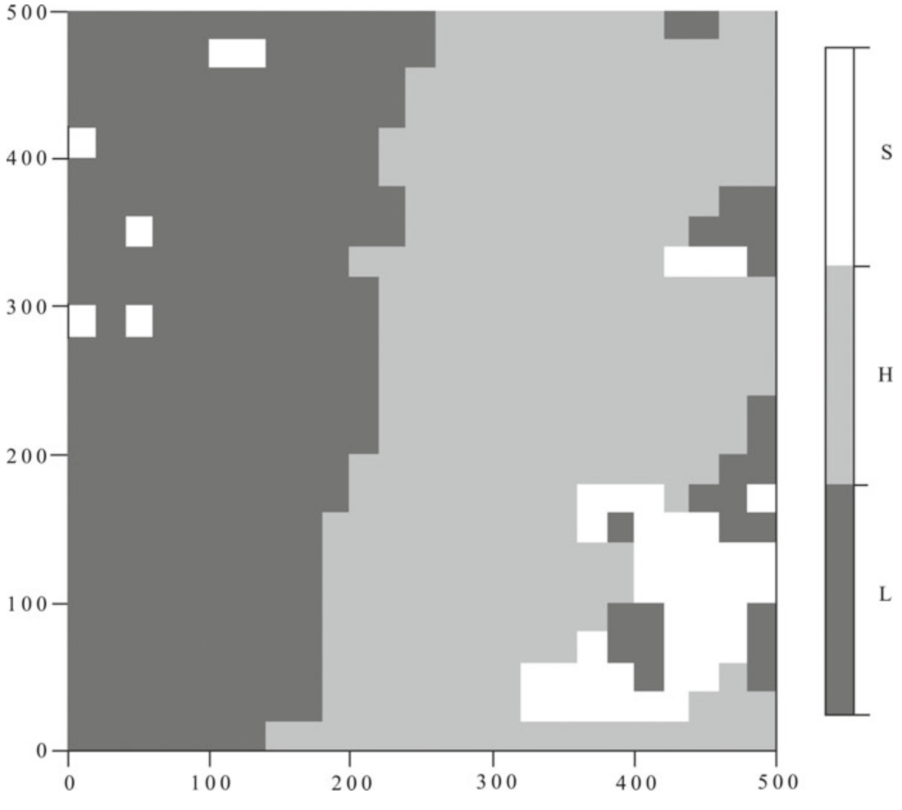

Fig. 2 Topographic map of 25-ha plot based on 20 m × 20 m grid. L represents low-plateau, H high-plateau and S slope. The same below.

of hypsographies (Fig. 1). All of the 625 20 m × 20 m quadrats of the plot could be unambiguously assigned to one of the three habitat categories (low-plateau, high-plateau and slope; Fig. 2). The number of grids of the high-plateau was the largest (*n* = 298), those of the low-plateau came in second (*n* = 281) and the

Table 1 Torus-translation test for habitat associations based on 20 m × 20 m scales on the 25-ha Forest Dynamics Plot of mixed temperate broad-leaved Korean pine forest in Changbai mountains in northeastern China. The results are habitat associations of 27 species with ≥ 50 stems by torus-translation test. The total includes all stems with DBH ≥ 1 cm. Saplings refer to trees with DBH ≤ 10 cm and shrubs with DBH ≤ 2 cm. Adults refer to trees with DBH > 10 cm and shrubs with DBH > 2 cm. Topography: L (low-plateau), H (high-plateau), S (slope). '+' indicates significant positive association and '–' indicates significant negative association (α = 0.05 for test). *Viburnum sargenti* is eliminated because DBH of all stems < 2 cm when comparing the habitat associations at adult and sapling stages.

Species	Habitat association		
	Total	Saplings	Adults
Trees			
Acer mandshuricum			
Acer mono	L+	L+/H–	
Acer pseudo-sieboldianum	L–	L–	L–/S+
Acer tegmentosum	H+		H+
Acer triflorum	H–	H–	H–/S+
Betula platyphylla		L+	
Fraxinus mandshurica	L+	H–	L+
Maackia amurensis			L+/H–
Malus baccata			
Phellodendron amurense			
Pinus koraiensis	S–		H+/S–
Prunus padus	L+/H–	L+/H–	
Pyrus ussuriensis	L+	L+	L+/H–
Quercus mongolica		L+/H–	
Tilia amurensis			L–/H+/S–
Tilia mandshurica	S+	S+	S+
Ulmus japonica			L+/H–
Ulmus laciniata	S+	S+	
Shrubs			
Acer barbinerve	L–	L–	
Acer ginnala	L+/H–	L+/H–	L+/H–
Acer tsckonoskii			L+
Corylus mandshurica			
Crataegus maximouwiczii			
Philadelphus schrenkii	L+	L+	
Rhamnus ussuriensis			L+
Syringa reticulata	L+/H–	L+/H–	L+/H–
Viburnum sargenti	H–		

number of slope grids was the smallest (n = 46).

4.2 Habitat associations within the 25-ha plot in the Changbai mountains

Many species were apparently distributed in a biased fashion with respect to habitats and 15 out of 27 species showed strong positive or negative association with specific habitats (Table 1). There were 7 species positively and 2 species negatively associated with the low-plateau habitat, 1 species positively and 5 species negatively associated with the high-plateau habitat, while 2 species were positively and 1 species negatively associated with slope habitat (Fig. 3). Eight species showed significantly negative association with their specific habitat (Fig. 3). *P. koraiensis*, one of the dominant species, showed significant negative association with slope habitat (Table 1). Nevertheless, *Q. mongolica* and *T. amurensis*, the other two dominant species, had no apparent habitat bias. *P. padus*, *A. ginnala* and *S. reticulate* expressed obvious association with two types of habitat. *T. mandshurica*, *U. laciniata* and *P. koraiensis* were significantly associated with slope habitat. The most frequently occurring species,

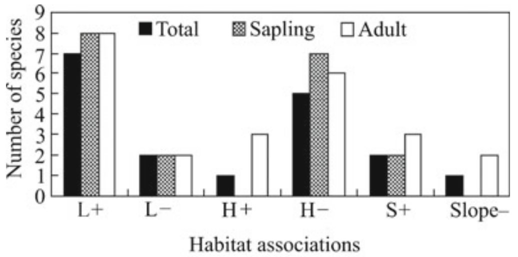

Fig. 3 Number of species associated with each of three habitat types on the 25-ha Forest Dynamics Plot of mixed temperate broad-leaved Korean pine forest in the Changbai mountains. The total shows all stems with DBH ≥ 1 cm. Saplings refer to trees with DBH ≤ 10 cm and shrubs with DBH ≤ 2 cm. Adults refer to trees with DBH > 10 cm and shrubs with DBH > 2 cm. '+' indicates significant positive association and '–' indicates significant negative association (α=0.05 for test).

i.e., *C. mandshurica*, showed no obvious bias with habitat.

4.3 Changes of habitat associations at sapling and adult stages

Most species showed different habitat associations at sapling and adult stages. Some species showed significant association with some specific habitats, others showed nothing at all at the sapling and adult stages. Only 3 out of 26 species showed the same habitat bias at the sapling and adult stages (Table 1). Five species had no obvious habitat associations at the two stages. The dominant species, *P. koraiensis,* was not significantly associated with a specific habitat at the sapling stage, but showed a clear bias to high-plateau habitats and avoided the slope habitat at the adult stage. *T. amurensis* showed clear preference for high-plateau habitats and disliked the low-plateau and slope habitats at the adult stage. Two species were negatively associated with the low-plateau, seven species excluded the high-plateau and no species avoided the slope at the sapling stage. Two species appeared to avoid the low-plateau, 6 species the high-plateau and 2 species shunned slopes at the adult stage (Fig. 3). Eight species appeared strongly and positively associated with the low-plateau at the sapling and adult stages. Two species showed a strong preference for the high-plateau and slope at the adult stage. Two species appeared biased towards the slope, while no species seemed to like the high-plateau at the sapling stage (Fig. 3).

4.4 Strength of habitat associations at sapling and adult stages

Adjusted density values indicated few species exhibited extremely strong habitat associations. Only 9 species had adjusted densities > 3 in the habitat for which they had a strong and positive affinity, as well as 6 species at the sapling stage and 7 species at the adult stage. In contrast, most species exhibited weak affinities, with adjusted densities of < 0.2 in their associated habitat types (Fig. 4). When the adjusted densities < 0.3, we can consider that the species are strongly inclined to avoid these habitats. Seven species showed typically negative affinities for a habitat, especially *T. mandshurica*, *A. mandshuricum* and *V. burejaeticum* whose adjusted densities were zero. The most strongly associated species was *S. reticulata*, with an adjusted density of 7.68 in the slope habitat at the adult stage (Fig. 4).

4.5 Habitat division and habitat-associations test

Habitat division was our first step for studying species-habitat associations. Some studies directly used topographic variables to compare factors such as elevation, convex and concave borders and slope (Beatty, 1984; Sri-Ngernyuang et al., 2003). The use of this method allowed for unequivocal between-site comparisons. Another advantage was that the method could distinguish the relative importance of elements that characterize topography. But many topographic variables (such as convex and concave borders and slope) were calculated from their elevation. Elevation of subquadrats were associated with many topographic variables. Furthermore, several topographic variables usually together contributed to species distribution for which, in practice, we could not intuitively judge species-habitat associations by the method of model topographic variables. Other studies classed topographic variable into several habitats according to certain rules (Harms et al., 2001; Valencia et al., 2004). Hence, we used the latter method for judging habitat associations intuitively.

Most statistical tests required that the sampling units be independent. However, many studies had illustrated that most tree species displayed a patchy distribution pattern (Condit et al., 2000) and the abundance of different tree species in continuously arranged sampling units were spatially autocorrelated (Roxburgh and Chesson, 1998; Webb and Peart, 2000), where spurious statistical associations between species and topography may have occurred due to coincidental similarity between spatial structures of populations and topography, since both tree species and topography showed spatially autocorrelated patterns of distribution. This meant that the assumption of randomness was violated and thus traditional statistical tests could not be applied (Roxburgh and Chesson, 1998; Webb

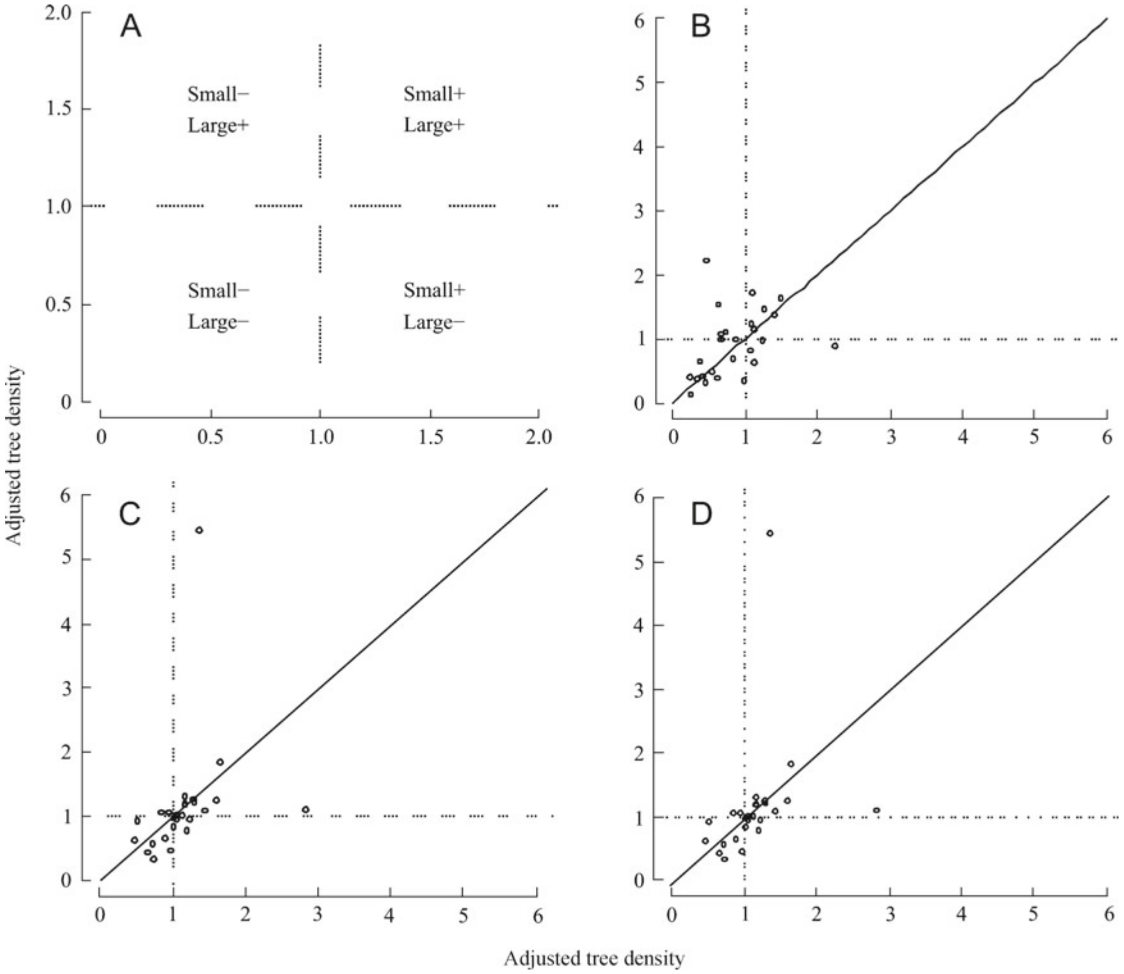

Fig. 4 Adjusted density of saplings and adults of 26 species in the low-plateau (B), high-plateau (C) and slope (D) habitats of the 25-ha Forest Dynamic Plot in the Changbai mountains. Adjusted density values > 1 indicate a positive affinity for the habitat, while values < 1 indicate a negative affinity for the habitat (see panel A). Black filled circles represent species that were significantly associated with the habitat at the sapling or adult stage.

and Peart, 2000). Torus-translation tests are available for testing species-habitat associations which are more conservative than Chi-square tests (Harms et al., 2001).

4.6 Species-habitat associations

The results show that many tree species vary greatly in their habitat associations in a typical temperate forest. We detected that 15 (55.6%) out of 27 abundant species showed significant associations with at least one habitat (torus-translation tests; Table 1). The percentage of associations appeared to be lower than percentages reported from some tropical forests. Association percentages in several studies were: 64% of the 171 most abundant species in a rain forest in Panama (Harms et al., 2001), 65% of 17 *Lauraceae* species in a Thai montane forest (Sri-Ngernyuang et al., 2003) and 8 out of 10 *Sterculiaceae* trees in a Bornean rain forest (Yamada et al., 2006). On the whole, the results of habitat associations from our mixed temperate forest were weaker than those of tropical forests, although different study methods could partially contribute to these differences, such as habitat division (our plot was only divided into three habitat types, while BCI plots were divided into five types) and statistical tests (we used torus-translation tests, where Sri-Ngernyuang et al. (2003) used discriminatory tests). As well, we had not considered the case of rare species. Some rare species possibly preferred some special habitat because of some special environmental conditions. In our plot, 17 (32.7%) out of 52 species were rare species (as per definition by Hubbell and Foster (1986); a species whose density was equal to or less than one tree per ha was considered rare), but we could not test their habitat associations for statistical reasons. We possibly weakened the species habitat associations by only analyzing the more common species.

4.7 Comparisons of sapling and adult habitat associations

For the 26 common species examined by us, we detected 22 (84.6%) significant species associations with one of the three habitats at the sapling or adult stage. Despite the occurrence of the same number of associations at the two stages, associations were seldom consistent across stages. Only 3 out of 22 associations with a specific habitat appeared to be consistent at the two stages. Similarly, Webb and Peart (2000) found only 2 out of 22 species showed associations with the same habitat at the seedling and adult stages in a forest in Borneo. Paoli et al. (2006) also found that only 2 out of 16 Dipterocarp species were significantly associated with the same habitat at the juvenile and adult stages in Borneo. In a study of habitat associations in a tropical forest, only 5 out of 30 species significantly associated with a habitat were associated with the same habitat at the small tree and large tree stages (Comita et al., 2007). These results indicate that few species show consistent associations with the same habitat across the life stages in tropical and temperate forests. Otherwise, comparisons of adjusted densities at the sapling and adult stages reveal that few species show opposite habitat associations at the different stages (Fig. 4).

4.8 Habitat associations with species coexistence

Most studies on species-habitat associations support the idea that species-habitat associations can turn into species coexistence (Harms et al., 2001; Sri-Ngernyuang et al., 2003; Paoli et al., 2006; Comita et al., 2007). How much do species-habitat associations contribute to species coexistence? Pulliam (1988) speculated that source-sink population dynamics exist. Harms et al. (2001) considered whether negative associations can be used to identify sink subpopulations. If so, the list of species not or positively associated with a particular habitat type would be equal to the number of species capable of sustaining populations if the plot was composed of only that one habitat type. They found that 20 (11.7%) out of 171 species were negatively associated with a swamp habitat and concluded that focal habitat specialization played a limited role in the maintenance of species diversity. However, Yamada et al. (2006) deemed that the conclusion of Harms et al. (2001) underestimated the true number of negative associations. They proposed that positive associations can be used to identify source subpopulations and that both neutral and negative species-habitat associations can be used to identify subpopulations that were maintained by the process of recruitment from the source subpopulations. Their results showed 8 (80%) out of 10 species were positively associated with a habitat, indicating that species-habitat associations contributed to the equilibrium coexistence in the Lambir forest. Our results show that 10 (37%) out of 27 species were positively associated with a habitat and 8 (29.6%) had a negative association. Whichever supposition, according to Harms et al. (2001) or Yamada et al. (2006) is accepted, our results show that species-habitat association can contribute to species coexistence. For example, *A. mandshuricum*, *A. mono*, *A. pseudo-sieboldianum*, *A. tegmentosum* and *A. triflorum* show different habitat associations among the tree species in our study (Table 1). Therefore, species-habitat associations have the effect of reducing the confamilial competition and contribute to the equilibrium coexistence of *Aceraceae* tree species in the mixed broad-leaved Korean pine forests of the Changbai mountains.

Studies of the species-habitat associations at different life stages are necessary. Habitat associations are size-class dependent (Webb and Peart, 2000). From our results we conclude that only 8 out of 26 species show the same habitat associations for all individuals, saplings and adults (5 species were neutral, *T. mandshurica* showed positive association with slope habitat, *A. ginnala* and *S. reticulata* showed positive association with the low-plateau habitat and negative association with the high-plateau habitat). The entire spectrum of species-habitat associations concealed changes in habitat associations at the different stages (Table 1). Most species showing inconsistent habitat associations at the two stages indicate that habitat associations can contribute to regeneration niches, further affecting species coexistence (Table 1). However, most species show a trend of similar habitat associations at the sapling and adult stages and changes appear small or moderate over their lifetime (Fig. 4), which revealed that regeneration niches, due to habitat associations, play a limited role in species coexistence. This is consistent with the conclusion of Comita et al. (2007) for the Panama forest. So, rather than focus on regeneration niche differences, theories of coexistence should consider more the importance of niche shifts during a lifetime.

5 Conclusions

The homogeneous environment of our study area includes many micro-habitat types, which can affect species coexistence. Species-habitat associations exit in the temperate forest of our 25-ha plot in the Changbai mountains. Owing to restricted statistical methods, our results partly underestimate the associations, since we ignored rare species. Hence, our observations of the performance of species in different habitats, coupled with experiments manipulating seed and sapling distributions, would provide further understanding of processes driving the observed patterns of habitat associations. Most species have no consistent association with their habitat at different stages of their existence, which shows that regeneration niches can contribute to coexistence. However, regeneration niches due to habitat associations play a limited role in species coexistence, since most species show a similar trend in habitat associations at the sapling and adult stages, when comparing the strength of habitat associations. We should pay more attention to shifts in habitat associations, i.e., niche shifts at different stages.

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