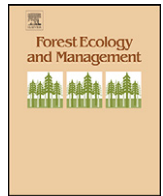




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Fine-scale species co-occurrence patterns in an old-growth temperate forest

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ABSTRACT

The pattern of species co-occurrence is instrumental for understanding community assembly rules. In this paper, we analyzed the co-occurrence of tree species in a 25-ha old-growth temperate forest plot in Northeastern China. The analysis was conducted at seven scales from 5 m × 5 m up to 100 m × 100 m in order to determine the patterns of co-occurrence at different spatial scales. Our analyses were conducted for all species, species with larger abundances, species with larger sizes, and five phylogenetic-based species groups. Our results showed that at smaller scales, the co-occurrence patterns of all species, species with larger abundances, and species with larger sizes were significantly higher than expected by chance, suggesting that strong interspecific competition exists in the community. At larger scales, there was no significant difference compared to randomized matrices. The result indicated that plant assembly rules are only found at small spatial scales. However, when co-occurrence metrics were restricted to phylogenetic groups, we could not find any clear evidence of interspecific competition within these groups. In conclusion, we found that competition is an important assembly rule at small scales in governing tree communities of our temperate forest, although it is not the only process involved. The importance of other processes should also be taken into account to explain species co-occurrence patterns.

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1. Introduction

Species co-occurrence analyses are increasingly applied to evaluate whether communities are random assemblages of species or the result of deterministic mechanisms, such as competition (Gotelli and McCabe, 2002; Jenkins, 2006; Adams, 2007) or other processes (Chen and Bradshaw, 1999; North et al., 2004; Ward and Beggs, 2007). Over three decades ago, Diamond (1975) described “checkerboard” distributions of avian species in the Bismarck Archipelago that never co-occurred, and predicted that competing species among assemblages should co-occur less than expected by chance. That study sparked a heated controversy in that the significance, or even the existence, of assembly rules was questioned (Gotelli and Graves, 1996; Adams, 2007). Connor and Simberloff (1979) argued that assembly rules could not be inferred from observed patterns by comparing the patterns with those generated by Monte Carlo null models. Since then, contrary conclusions have been drawn from different communities. Gotelli and McCabe (2002) conducted a meta-analysis of published data matrices, and found that nonrandom co-occurrence patterns are prevalent. Using a database of 45 species and 4540 geographic

sites, Adams (2007) analyzed the patterns of co-occurrence by virtue of a null model derived from competitive interactions, and found that patterns of co-occurrence were significantly nonrandom at both regional and continental scales, providing strong evidence for competitive-based community assembly. Nonrandom species co-occurrence patterns can vary with niche differentiation (Hofer et al., 2004), spatial scale (Gotelli and Ellison, 2002), temporal scale (Badano et al., 2005), and assemblage diversity (Badano et al., 2005; Mouillot et al., 2005). However, recent work on ectoparasites in fish (Jackson et al., 1992; Gotelli and Rohde, 2002), birds (Feeley, 2003), and zooplankton (Jenkins, 2006) found little support for nonrandom species co-occurrence patterns.

Scale is an important factor for studying species co-occurrence (Bycroft et al., 1993; Chen and Bradshaw, 1999; Jenkins, 2006; Sanders et al., 2007). Co-occurrence can exhibit one pattern at one scale, but a different pattern at another scale. Although there are many studies comparing of co-occurrence patterns between local and regional scales (e.g., Gotelli and Ellison, 2002; Jenkins, 2006; Sanders et al., 2007), little has been mentioned of co-occurrence patterns at fine neighborhood scales. Wilson et al. (1992) argued that evidence for plant community structure can be found mainly, perhaps only, at a small spatial scale. The analyses of fine-scale co-occurrence patterns can give us important information about assembly mechanisms (Bycroft et al., 1993).

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In this paper, we analyzed fine-scale species co-occurrence in a 25-ha old-growth temperate forest, Northeastern China in order to understand the importance of competition in structuring the tree community. Co-occurrence analyses were conducted for all species, species with larger abundances, species with larger sizes, and phylogenetic-based species groups. Three questions were addressed in this paper: (1) what are species co-occurrence patterns in the old-growth temperate forest? (2) Does scale play a key role for species co-occurrence in the forest? And how do assembly rules change with scales? (3) Are the co-occurrence patterns consistent with co-occurrence patterns structured by competition?

2. Methods

2.1. Study site

The study site is located in the Changbai Mountain Nature Reserve, which was established along the border of China and North Korea extending from 127°42' to 128°17'E and 41°43' to 42°26'N. The reserve was established in 1960 and joined the World Biosphere Reserve Network under the Man and the Biosphere Project in 1980. The reserve is about 200,000 ha in size and elevation ranges from 740 m at the lowest part to 2691 m at the summit of Changbai Mountain on the Chinese side. There are five typical vertical vegetation zones, namely aspen-white birch (*Populus davidiana* and *Betula platyphylla*) forest, broad-leaved Korean pine (*Pinus koraiensis*) mixed forest, spruce-fir (*Picea jezoensis* and *Abies nephrolepis*) forest, subalpine birch (*Betula ermanii*) forest and the tundra (Yang et al., 1985; Hao et al., 2007).

Our study site is located in the broad-leaved Korean pine mixed forest, a conifer broad-leaved mixed temperate forest, which is the most common vegetation type in northeastern China. It is well known for its high biodiversity, complex stand structure, and unique species composition. The soil is classified as dark brown forest soil. The climate is characterized by the moist temperate monsoon. Mean annual temperature is 3.3 °C (January –16.5 °C and August 20.5 °C). Mean annual precipitation is 671.9 mm year⁻¹, most of which occurs between June and August. The stand age is about 300 years. Vertical structure of the forest can be identified (Hao et al., 2007). The canopy layer is >20 m tall, and the main tree species are Korean pine, Amur linden (*Tilia amurensis*), Mongolian oak (*Quercus mongolica*), Manchurian ash (*Fraxinus mandshurica*), and Japanese elm (*Ulmus japonica*). Main species of the midstory layer (10–20 m tall) include Mono maple (*Acer mono*), Purplebloom maple (*A. pseudo-sieboldianum*), Manchustriple maple (*A. tegmentosum*), Amur Maackia (*Maackia amurensis*). Understory layer is below 10 m, includes Manchurian Hazelnut (*Corylus mandshurica*), Barbedvein maple (*A. barbinerve*), European Bird Cherry (*Prunus padus*) and so on.

A 25-ha (500 m × 500 m) plot was established in 2004. The plot was chosen in the core zone of the reserve in order to avoid human disturbances (Hao et al., 2007). All individuals with DBH ≥ 1 cm were stem-mapped, and identified to species. There are 38,902 living stems, belonging to 52 species, 32 genera, and 18 families. Mean stand density of living trees was 1556 trees ha⁻¹, and mean basal area of living trees was 43.2 m² ha⁻¹ (Hao et al., 2007; Zhang et al., 2007).

2.2. Data analysis

We divided our study plot into 10,000, 2500, 625, 256, 100, 49, and 25 quadrats at seven scales: 5 m × 5 m, 10 m × 10 m, 20 m × 20 m, 30 m × 30 m, 50 m × 50 m, 70 m × 70 m, and 100 m × 100 m, respectively. Presence-absence data matrices were attained from the abundance data sets based on the quadrats

at the seven scales. In each presence-absence matrix, each row represents a species and each column represents the presence (1) or absence (0) of a species in a sample (or site). Fifty-two species were included for the co-occurrence analyses of all species.

Similarly, the plot data were transformed to presence-absence matrices for the species with restricted species abundance classes (≥100, ≥500, and ≥1000 stems, respectively), the species with larger size classes (DBH ≥ 10 cm, 20 cm, and 30 cm, respectively), and the species group based on phylogeny in order to analyze the co-occurrence in each case. The species with high abundances were chosen to avoid the “dilution effect” (Gotelli and Graves, 1996). The species of different size classes were chosen in order to test if competition changes with size classes. Phylogenetic data of 52 species in our plot were obtained by Phylomatic (R20050610.new, <http://www.phylodiversity.net/phyloomatic/>), which is based on the work of the Angiosperm Phylogeny Group (Stevens, 2001). Five species groups were chosen by phylogenetic-based classification, and related co-occurrence indices were calculated for each species group.

Analyses of presence-absence matrices with “null model” randomization tests and co-occurrence indices have been the standard method for measuring co-occurrences (e.g., Gotelli and Ellison, 2002; Bell, 2005; Jenkins, 2006; Adams, 2007; Burns, 2007), although there remains disagreement about what null model and index should be used. In this paper, species co-occurrences were calculated by using four indices: the checkerboard score of matrix (C score), the number of checkerboard species pairs (CHECKER), the number of species combinations (COMBO), and the variance ratio (V ratio). Their measures and performance were described in detail in Gotelli (2000). If an assemblage is structured by competition, observed communities should contain a larger C score, more checkerboard pairs, fewer species combinations, and lower V ratio than expected by chance (Gotelli and Ellison, 2002). We used a fixed-equiprobable null model (SIM2 of Gotelli (2000)) to generate the randomly constructed assemblages. In this null model, row sums are fixed in order that each species occurs with the same frequency in the randomly constructed assemblages as in the observed assemblage, while all columns are equiprobable (Gotelli and Entsminger, 2006). Gotelli (2000) found that fixed-equiprobable null model seems most appropriate for analyzing “sample lists”, particularly when comparing standardized samples that have been collected in areas of homogenous habitat which is largely the condition of our 25-ha plot (unpublished data). In the study plot, the terrain is relatively gentle. The elevation ranges from 791.8 m to 809.5 m, with a mean elevation of 801.5 m. The sequential swap algorithm was used for randomization.

To make the results comparable, we calculated a standardized effect size (SES) for each matrix (Gurevitch et al., 1992). The SES is calculated as: (observed index – mean of simulated index)/standard deviation of simulated index. Assuming a normal distribution of SES, a 95% confidence interval of the SES values should locate between –2.0 and 2.0. For the C score and the CHECKER, the values larger than 2.0 indicate nonrandom species segregation, and the values lower than –2.0 indicate nonrandom species aggregation. In contrast, for the COMBO and the V ratio, the values larger than 2.0 indicate nonrandom species aggregation, and the values lower than –2.0 indicate nonrandom species segregation. The mean and standard deviations of these indices were calculated from 5000 null randomization matrices. Co-occurrence analyses and associated randomization tests were calculated from 5000 null matrices by using null model software EcoSim 7.72 (Gotelli and Entsminger, 2006).

To explore whether the competition exists among different guild groups and within them and how they change with scales, we used the “Guild structure” module in EcoSim for patterns among the

guilds as a group (Gotelli and Entsminger, 2006). The same five phylogenetic groups were used for the analyses at seven scales. The method tests whether the mean co-occurrence index among guild groups is larger or smaller than expected by chance and tests the variance of the co-occurrence index among guild groups. Mean-time, the favored states hypothesis was tested in this module (Fox and Brown, 1993). This hypothesis assumes that the distribution of species among guilds, or even among communities, is more uniform than predicted by a random distribution. If communities are formed by sequentially adding species in different functional groups, there should be a significantly larger number of favored states than expected by chance (Gotelli and Entsminger, 2006). The mean and standard deviations of the same indices with co-occurrence analyses were calculated from 5000 null matrices, and the SES values were calculated for the related comparison.

3. Results

3.1. Co-occurrence patterns of the community

Community-wide co-occurrence patterns varied with scales (Fig. 1). At 5 m and 10 m scales, the observed C score of all species were significantly higher than expected by chance, suggesting a negative pattern of species co-occurrence. The positive co-occurrence patterns of all species were captured at 30 m and 50 m. The checkerboard patterns (the index CHECKER) cannot be found at all observed scales. For the co-occurrence index COMBO (the numbers of species combinations), the observed values of all species were significantly lower than expected by chance at scales 5–30 m, indicating a strong negative association, which are likely to be the result of interspecific competition. The V ratio of all species measures the variability in the number of species per site. There is no significant value found at small scales, whereas values larger than expected by chance occurred at scales of 20–70 m. In addition, the highest values of C score and COMBO for all species occurred at a scale of 10 m, suggesting that the strongest interspecific competition exists at the scale.

Nonrandom co-occurrence patterns were found at small scales, and there is no significant difference compared to randomized matrices at large scales, when we measured the co-occurrence by restricting to higher species abundance and larger tree sizes (Figs. 1 and 2). To the species with higher abundances, the observed C score and COMBO showed significantly higher values than expected by chance at small scales, which were similar with the co-occurrence pattern of all species. And there were the highest C scores for three abundance levels at scale 10 m, and the highest COMBO for abundance ≥ 100 and ≥ 500 at scale 10 m, suggesting that strong interspecific competition occurs at the scale. The V ratio did not show evidence of nonrandom co-occurrence patterns. For the species at three size classes, similar co-occurrence patterns were found in the four co-occurrence indices (Fig. 2).

3.2. Co-occurrence patterns of different phylogenetic groups

The co-occurrence patterns for the five phylogenetic groups differed largely with the co-occurrence patterns of the community (Fig. 3). We could not find any clear evidence for interspecific competition within these groups. The hypothesis that phylogenetic groups may experience greater interspecific competition because of their ecological similarity cannot be validated. For the four indices, the co-occurrence of two groups showed positive association at 5 m and 10 m scales, which are likely to be the result of interspecific facilitation. For the indices C score and V ratio, the co-occurrence of one group showed positive association at 5–50 m.

For the four co-occurrence indices, the unusually large variances were captured at all scales, when we analyzed the co-occurrence patterns among the five phylogenetic groups (Table 1). The large variances suggested that there were significant differences in their levels of co-occurrence. The same results also were found when we analyzed the co-occurrence within each group (Fig. 3). In the favored states analyses, SES of the four indices did not show significant difference compared with that expected by chance.

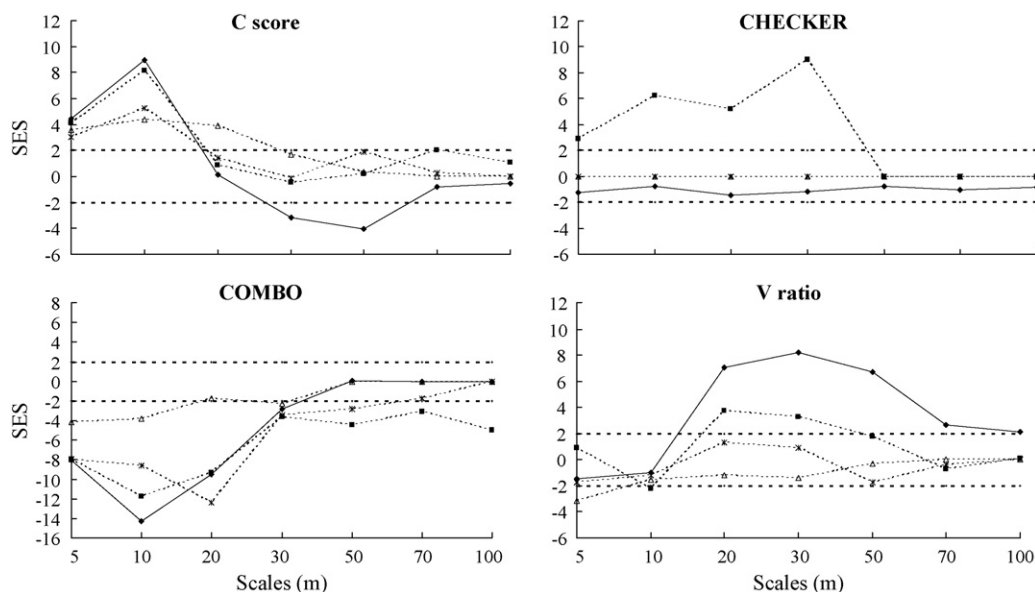


Fig. 1. The co-occurrence patterns of all species and species with larger abundances (≥ 100 , ≥ 500 , and ≥ 1000 individuals, respectively) at seven spatial scales in a 25-ha old-growth temperate forest plot in northeastern China. Standardized effect sizes of four co-occurrence indices were calculated with null model software EcoSim 7.72. For the checkerboard score of the matrix (C score) and the number of checkerboard species pairs (CHECKER), the values larger than 2.0 indicate nonrandom species segregation, and the values lower than -2.0 indicate nonrandom species aggregation. For the number of species combinations (COMBO) and the variance ratio (V ratio), the values larger than 2.0 indicate nonrandom species aggregation, and the values lower than -2.0 indicate nonrandom species segregation. Bold lines with diamond symbols represent all species, while broken lines with solid square, asterisk, triangle point-up symbols represent the species with abundances ≥ 100 , ≥ 500 , and ≥ 1000 , respectively.

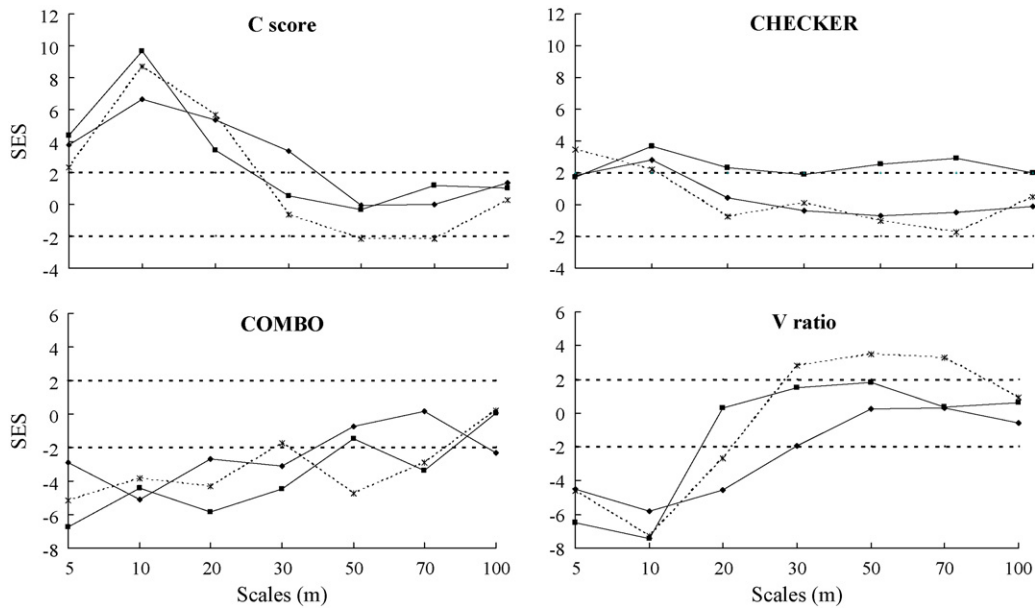


Fig. 2. The co-occurrence patterns of species at three size classes, DBH ≥ 10 cm (bold lines with square), DBH ≥ 20 cm (broken lines with asterisk), and DBH ≥ 30 cm (bold lines with diamond), respectively. Other explanations are the same as in Fig. 1.

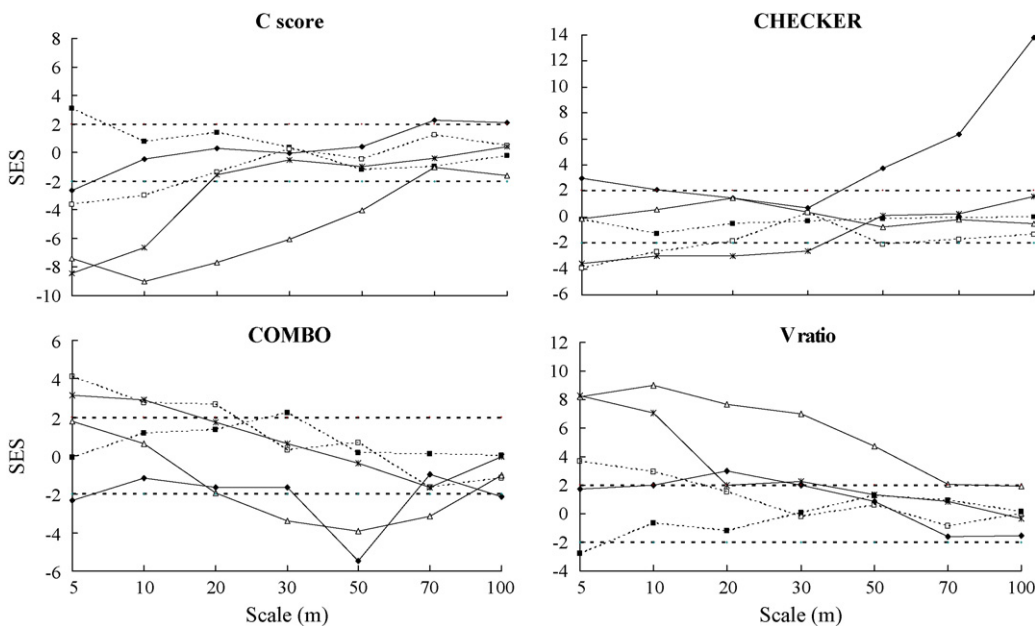


Fig. 3. The co-occurrence patterns of five species groups by phylogenetic-based classification. Other explanations are the same as in Fig. 1.

Table 1
The co-occurrence patterns among five phylogenetic groups in the study plot. The patterns were analyzed using the “Guild structure” module in EcoSim. Standardized effect sizes were used in order to test whether the mean co-occurrence index among guild groups is larger or smaller than expected by chance, and the variance of the co-occurrence index among guild groups. An unusually large variance would mean that the guild groups differ significantly from one another in their levels of co-occurrence, while an unusually small variance would mean that guilds are strikingly similar to one another in the level of co-occurrence observed. If communities are formed by sequentially adding species in different functional groups, there should be a significantly larger number of favored states than expected by chance. Other explanations are the same as in Fig. 1.

Scales	SES of C score		SES of CHECKER		SES of COMBO		SES of V ratio	
	Variance	Favored states	Variance	Favored states	Variance	Favored states	Variance	Favored states
5 m × 5 m	-6,117,606,000	-1.04	-157.03	-1.01	-714.75	-1.03	2.81	-1.04
10 m × 10 m	-923,182,100	-1.02	-116.73	-1.04	-2170.44	-1.04	2.93	-1.04
20 m × 20 m	-3,519,734	-0.63	-77.98	-0.61	-776.74	-0.62	1.97	-0.60
30 m × 30 m	-91,478.58	-0.41	-58.50	-0.42	-371.39	-0.42	2.38	-0.41
50 m × 50 m	-5,766.67	-0.39	-31.86	-0.40	-182.63	-0.39	1.59	-0.38
70 m × 70 m	-579.57	-0.29	-19.95	-0.30	-58.12	-0.30	0.88	-0.31
100 m × 100 m	-50.45	-0.29	-12.69	-0.29	-14.47	-0.29	0.66	-0.28

4. Discussion

According to our analyses, the community exhibited less species co-occurrence patterns than expected by chance at small spatial scales, which partly supported the predictions of Diamond's (1975) assembly rules model. The same result has been reported in several other studies (e.g., Watkins and Wilson, 1992; Gotelli and McCabe, 2002; Swenson et al., 2006; Adams, 2007; Sanders et al., 2007). Our analysis also showed that at larger spatial scales, the community did not show significant co-occurrence patterns. Similar results were obtained when the co-occurrence patterns were analyzed both for species of higher abundance and trees of larger size.

A major effort of community ecology is to document nonrandom patterns of coexisting species and to infer about underlying processes or assembly rules that may have given rise to the observed patterns (Gotelli and Graves, 1996; Sanders et al., 2007). For a long time, nonrandom co-occurrence patterns were interpreted to result from interspecific competition for essentially the same set of mineral resources, light and water (Diamond, 1975; Kelt and Brown, 1999; Tilman, 2007; Hanski, 2008). Diamond (1975) emphasized that interspecific competition was the most important determinant of observed species combinations and could lead to consistent rules regarding species organization and distribution. In our plot, strong interspecific competition may exist at small scales, evidenced by the nonrandom co-occurrence patterns (Figs. 1 and 2), consistent with the results of previous researches in the forest (Sun and Zhao, 1997; Hao et al., 2007; Zhang et al., 2007).

Random co-occurrence patterns were found at larger scales, in either community level or species with larger abundances or size classes, suggesting that there may be no dominant processes that influence species distribution of the plot. At larger scales, habitat heterogeneity was very small in our plot relative to many other forest plots (Hao et al., 2008). Compared with the results at small scales, we can conclude that spatial scale plays an important role in shaping community assembly rules, and co-occurrence patterns change with spatial scale (Bycroft et al., 1993; Chen and Bradshaw, 1999; Adams, 2007). In accord with Watkins and Wilson's (1992) argument, nonrandom co-occurrence in temperate forests can be found mainly at small spatial scales.

Co-occurrence patterns based on phylogenetic groups differed largely from the co-occurrence patterns of the community. There is no clear evidence for interspecific competition within the phylogenetic groups in the forest. Generally, phylogenetically related species with ecologically similar characters are likely to coexist less frequently than expected by chance because of limited resources (Kelt and Brown, 1999; Webb et al., 2002). Interspecific competition should be much stronger among these species, especially at small scales. However, we found that co-occurrence patterns of three groups showed significant positive associations at smaller scales, which are likely to be the result of interspecific facilitation. Similar results were also found in other communities (Wilson and Lee, 1994; Veech, 2006; Valiente-Banuet and Verdú, 2008). Similar habitat requirement and limited seed dispersal, which lead to clumped distribution of species, perhaps are two main factors caused the patterns (Helmus et al., 2007). There is no evidence for interspecific competition at large scales in the community. Maybe there are enough resources provided for the coexistence of these ecologically similar species. Meantime, we find that there are significant differences among these phylogenetic groups, suggesting some difference in ecological and evolutionary processes.

Additionally, several alternative explanations rather than competition for nonrandom co-occurrence patterns are possible. These include habitat heterogeneity (Ward and Beggs, 2007),

evolutionary history (Gotelli and McCabe, 2002), and even stochastic processes (Ulrich, 2004; Bell, 2005). In particular, habitat heterogeneity is an important factor for shaping nonrandom patterns at small scales (Ward and Beggs, 2007). We tried to remove this factor by restricting the analyses to one forest plot with homogeneous habitat. However, it is still possible that the differences of micro-habitat at small scales influenced species distributions. For example, some tree species in our forest, such as *T. mandshurica*, *U. laciniata*, *A. tegmentosum*, and *A. mandshuricum*, showed significantly positive or negative spatial associations with topographic conditions (Hao et al., 2008). Further studies are needed to link species co-occurrence patterns and habitat heterogeneity. Ulrich (2004) and Bell (2005) both found that the neutral model could generate nonrandom co-occurrence patterns predicted by Diamond's (1975) assembly rules model, which is based on niche differentiation and interspecific competition. The role of stochastic processes or chance for shaping species distribution remains to be explored in our forest.

In summary, we used a stem-mapped database from a 25-ha old-growth temperate forest plot to understand species co-occurrence at multiple spatial scales. Our results showed that the co-occurrence patterns of the community are closely related to spatial scales. At smaller scales, the co-occurrence patterns of the community were significantly higher than expected by chance, suggesting that strong interspecific competition may exist in the community. However, at larger scales, there was no significant difference compared to randomized matrices, which indicated that plant assembly rules are only captured at small spatial scales. When co-occurrence metrics were restricted to phylogenetic groups, we could not find any clear evidence of negative nonrandom co-occurrence patterns within these groups. Finally, we can conclude that competition should be an important assembly rule at small scales in structuring tree communities, although it is not the only process involved. The other processes, including habitat heterogeneity, evolutionary history, and stochastic processes, should also be taken into account to explain community assembly rules.

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