

Effect of competition on spatial patterns of oak forests on the Chinese Loess Plateau

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Abstract: Reforestation or natural forest regeneration is an alternative measure for controlling soil erosion in degraded land on the Chinese Loess Plateau (CLP). However, our understanding of the temporal dynamics and the spatial patterns of forest regeneration remains inadequate. Two oak forests at different development stages were investigated to determine the spatial patterns of competitions (intraspecies and interspecies) during different successional stages. The intraspecies and interspecies spatial relationships among different tree diameters at breast height were analyzed at multiple scales by Kriging interpolation method and univariate and bivariate O-ring statistics. Our analytical results indicated that self-correlation and competition intensity were relatively high between oak and pine trees in the early development stage of oak forests due to their clumped distributions of heavy seeds. Birch trees had a lower competition in comparison to oak trees although birch was the dominant species. Therefore, asymmetric competition of oak trees was most likely to have led to their edge dispersal and their success in replacing the pioneer species. Asymmetric competition means that larger individuals obtained a disproportionately large share of the resources and suppressed the growth of smaller individuals. Kriging interpolation analysis showed a tendency towards homogenization caused by interspecies competition during the succession of oak forests. Our results demonstrated that the competition was the driving factor in the spatial distribution of oak forests on the CLP.

Keywords: arid and semi-arid region; forest regeneration; competition; spatial pattern; oak forests

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1 Introduction

The Chinese Loess Plateau (CLP) is naturally vulnerable to soil erosion, with approximately 72.3% of the total $650 \times 10^3 \text{ km}^2$ land being subjected to severe soil erosion (Peng, 2013; Kang et al., 2014). The soil erosion on the CLP had been greatly exacerbated before the late-20th century by massive human activities such as land reclamation, deforestation and overgrazing (Zhao, 1991). The direct adverse consequences of soil erosion, naturally occurred or/and human induced, are intensive declines in land productivity and extensive reductions in vegetation coverage (Li et al., 2005; Qin et al., 2006; Shao et al., 2008; Wang et al., 2009; Guo and Wang, 2012; Peng, 2013).

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Among the human activities that had exacerbated the soil erosion on the CLP, deforestation, as well as the associated removal of non-forest vegetation was the most notorious (Zhao, 1991). It means that reforestation or natural forest regeneration can be an effective measure in controlling the soil erosion and thus in ameliorating the ecological environment on the CLP.

During reforestation or natural forest regeneration, internal competition among plants for limited resources has been proven to be the driving factor for the success of a forest succession (Tilman, 1994; Pillay and Ward, 2012; Fraver et al., 2014). For example, Zhang et al. (2015) found that the internal competition of a community drove the forest dynamics in western Canada while the external factors played a minor role. A number of models were proposed to elucidate the mechanisms of the internal competition. Followings are our brief critiques on some of those models. Grid-based models explained the interspecies competition but ignored the heterogeneity of resources (Goldberg and Barton, 1992). Tessellation models considered the forest as a homogenous unit but ignored the possible influence of the neighboring plant species (Berger et al., 2008). Distance-size models or Hegyi's models (Hegyi, 1974; Weiner, 1990) took account of the size and height of plant species (Sandoval and Cancino, 2008; Linkevičius et al., 2014; Saha et al., 2014), and these models did appreciate the complexity of the competing processes at different spatial scales (Houston et al., 1988; Berger et al., 2008).

Most published studies focused on the community composition and the soil factors in understanding reforestation processes, whereas research on the spatial patterns of tree competition at various development stages is still lacking (An et al., 2007; Li et al., 2008; Liang et al., 2010). This study took advantages of two large patches of *Quercus wutaishanica* (oak) forest (secondary forest) in Ziwuling Mountains on the CLP to investigate the spatial patterns of tree competition at various development stages using Hegyi's models (Kang et al., 2014; Sun et al., 2015).

2 Materials and methods

2.1 Study area and sampling

The study area is situated in Guandaogou Watershed of Ziwuling Mountains (36.08°N, 109.67°E; Fig. 1), the latter (Ziwuling Mountains) being the largest habitat of *Q. wutaishanica* on the CLP. The Guandaogou Watershed was once mainly covered with an aspen–birch mixed forest (*Populus davidiana* and *Betula platyphylla*) and the forest had begun to recover in the late-20th century after a continuous deforestation of over 100 years (Li and Shao, 2004). In this study, the early or original land cover/use data of the selected plots were obtained through interviews with local farmers and the late or recent land cover/use data were obtained from the reliably-sourced records. Two plots (50 m×50 m) with different forest development stages were selected (lower panel of Fig. 1). Plot 1 (1252 m a.s.l.), situated in the edge of the forest, was at early successional stages, in which *Q. wutaishanica* mixed with *P. davidiana* and *B. platyphylla*. Plot 2 (1290 m a.s.l.), situated in the center of the forest, was at late successional stages represented by a pure *Q. wutaishanica* forest. Within these two plots, all trees with the diameter at breast height (DBH, 1.3 m above ground level) greater than 4 cm or with the height greater than 2 m were measured. The species names, diameters, and heights of the measured trees were recorded, and the coordinate of each one of the measured trees in each plot was marked in a coordinate chart representing the 50 m×50 m plot that was divided into 5 m×5 m cells (upper panel of Fig. 1). The dominant trees in the studied plots were *Q. wutaishanica*, *B. platyphylla*, *Pinus tabuliformis*, *P. davidiana*, *Acer ginnala* and *Syringa reticulata* var. *amurensis*; dominant shrubs were *Campylotropis macrocarpa*, *Lespedeza bicolor*, *Rosa hugonis*, *Cotoneaster multiflorus* and *Lonicera maackii*; and dominant herbs were *Setaria viridis*, *Duchesnea indica*, *Carex lancifolia*, *Deyeuxia arundinacea* and *Thalictrum squarrosum*.

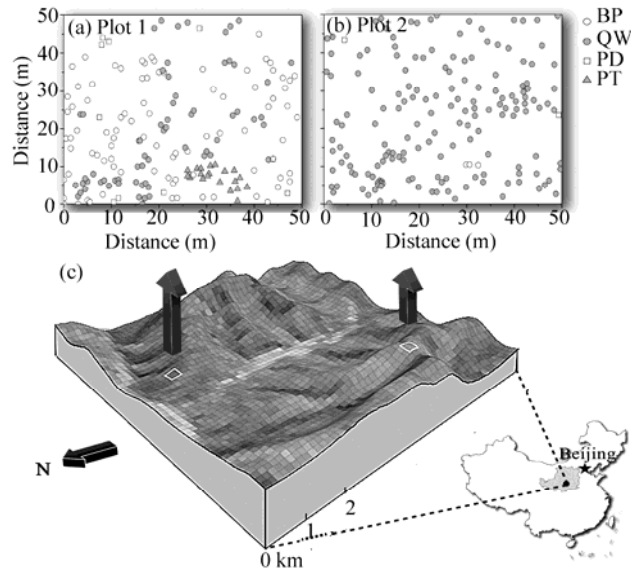


Fig. 1 Species distribution and topography of the two plots selected for this study. BP, *Betula platyphylla*; QW, *Quercus wutaishanica*; PD, *Populus davidiana*; PT, *Pinus tabulaeformis*.

2.2 Data processing

A competition index was proposed by Hegyi in 1974 to express the intensity of competition and the index differentiates the contribution of each one of the competing species during the successional stages of a community. The chosen index is modified from Hegyi's competition index, a distance-dependent index for individual trees (Hegyi, 1974):

$$CI_a = \sum_{n=1}^n \frac{S_n}{S_a D_{an}}. \quad (1)$$

Where CI_a is the Hegyi's competition index for tree a , N the number of neighbor competitor trees in the radius of 6 m (average crown diameter of oak forests in the plots) from the target tree; S_a and S_n are sizes (m) of target trees and competitor, and D_{an} the distance (m) between the target tree and the competitor.

The spatial distribution patterns, interspecies spatial relations with different sizes, and interspecies correlations of the main tree species were also analyzed at multiple scales using Kriging interpolation method and univariate and bivariate O-ring statistics. In geostatistics, the interpolated values of Kriging interpolation method are modeled by a Gaussian process governed by prior covariance, as opposed to a piecewise-polynomial spline chosen to optimize smoothness of the fitted values (Bayraktar and Turalioglu, 2005). O-ring statistic characterizes patterns by the frequency of points co-occurring at a given distance, so it can analyze the spatial patterns and interactions of trees species. Using rings (O-ring statistics) instead of circles (Ripley's K -functions) can effectively isolate the specific distance classes at a long-distance, whereas the Ripley's K -function can only be applied at shorter distance (Wiegand and Moloney, 2004). Univariate O-ring statistics can be used to analyze the spatial pattern of one object, while the bivariate O-ring statistics can be used to analyze the spatial association of two objects (Pattern 1 and Pattern 2). In this study, the univariate O-ring statistic was used to analyze the spatial patterns of tree species at different development stages of oak forests, and the bivariate O-ring statistic was used to analyze intra- and interspecies spatial associations among the tree species.

2.3 Data analysis

Automatic screening of target trees and competitors and CI (competition index) calculation were completed by R 3.2.0 software. Analysis of spatial distribution patterns was completed by Programita and Origin 8.5. Figures were plotted by ArcGis10.0 and Origin 8.52.

3 Results

Figure 2 shows that *P. tabulaeformis* (PT) and *Q. wutaishanica* (QW) had higher CI values than *B. platyphylla* (BP) and *P. Davidiana* (PD), suggesting an intensive competition between these two species (PT and QW) in the early development stages of oak forests. However, the fact that the CI values of nearly 70% the studied *Q. wutaishanica* trees were lower than the average CI value suggested that the CI-indicated intensive competition was probably skewed by a limited number of individuals of its population. Moreover, *B. platyphylla* also displayed a similar competition pattern with *Q. wutaishanica*, although *B. platyphylla* tree was a mild competitor. In the mixed forest, *P. davidiana* had the smallest number of trees and also the lowest CI value.

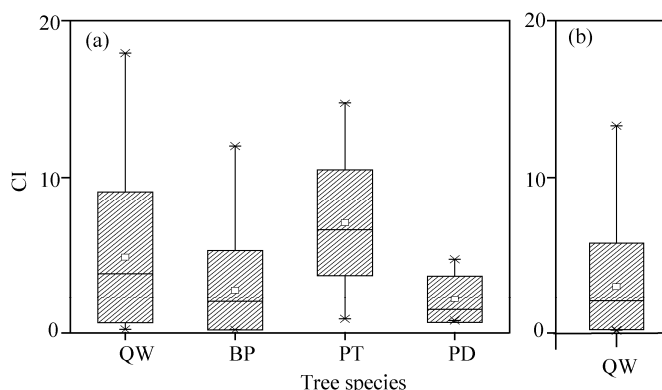


Fig. 2 Competition index (CI) of each tree species in the early (a) and late (b) development stages. QW, *Quercus wutaishanica*; BP, *Betula platyphylla*; PT, *Pinus tabulaeformis*; PD, *Populus davidiana* (Notes: Short lines above and below the boxes are the maximal values and minimal values; small white squares are the means; boxes are numerical ranges of CI between 25% and 75%; horizontal lines in the box are medians.)

A significant negative correlation between DBH (diameter at breast height) and CI (competition index) of each tree species in the early development stage of oak forests was found for all studied tree species (Figs. 3a–d) and the strongest negative correlation was shown in the species *P. tabulaeformis* ($R^2=0.43$; Fig. 3c). The overall relationship between DBH and CI for all of the four studied species was also negative ($R^2=0.21$; Fig. 3e), suggesting that the larger the trees, the less competitive they were, and that thus implying that the older the trees, the less competitive they were.

Figure 4 shows the spatially-distributed (i.e., Kriging-interpolated) CI values or the spatial distribution of CI values on the 50 m×50 m plots. A positive relationship between CI and tree density was found in both of the plots (Figs. 4a and b), implying that the forest with higher density was more competitive. Patches of high CI value were found in all development stages. The patches with high CI showed a wider range in the early development stage than in the late developmental stage, indicating that the competition intensity declined with forest development in the study area. However, the fact that the patches with high CI did not disappear in the late development stage indicated that long-term asymmetric competitions occurred in the oak forest during the succession process.

Interspecies and interspecies relationships among tree species in the early development stage were analyzed using univariate and bivariate O-ring statistics. Points higher than the confidence interval indicated clumped distributions or positive correlations; points lower than the confidence interval indicated segregated or overdispersed distributions or a negative correlation; points within the confidence interval suggested random distributions or no significant correlations (Kang et al., 2014). Figure 5 shows that *Q. wutaishanica* and *P. tabulaeformis* had significant self-correlation at small spatial scales, whereas no significant correlation was observed at large spatial scales. The spatial patterns of oak forests are associated with the biological characteristics of species. For instance, the heavy seeds of *Q. wutaishanica* were clustered at small-scales within the vicinity of the mother trees, and thus resulted in a clumped population. By contrast, *B.*

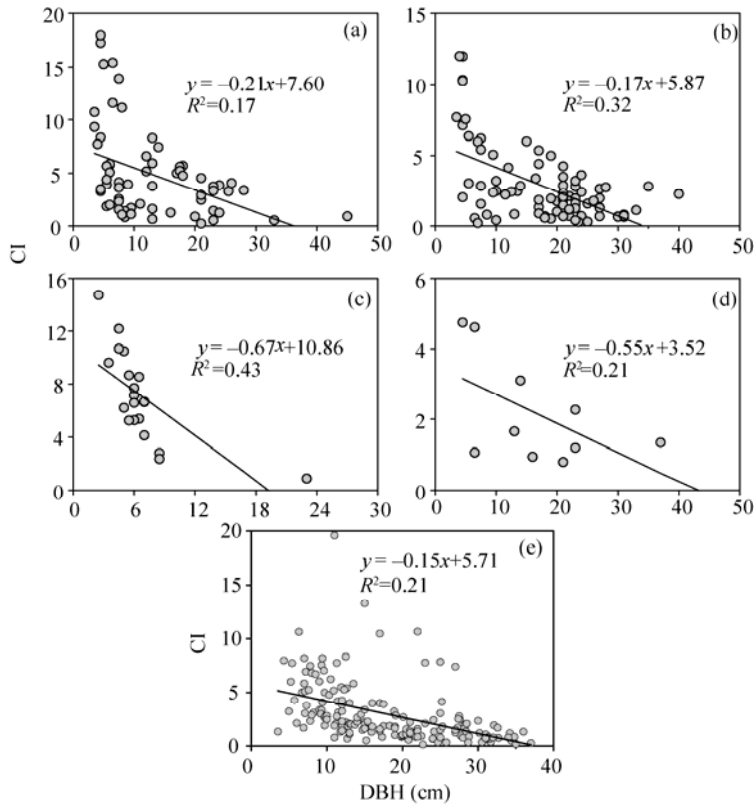


Fig. 3 Relationship between diameter at breast height (DBH) and CI (competition index) in the early (a, *Quercus wutaishanica*; b, *Betula platyphylla*; c, *Pinus tabulaeformis*; d, *Populus davidiana*) and late (e, *Quercus wutaishanica*) development stages of oak forests on the Chinese Loess Plateau (CLP)

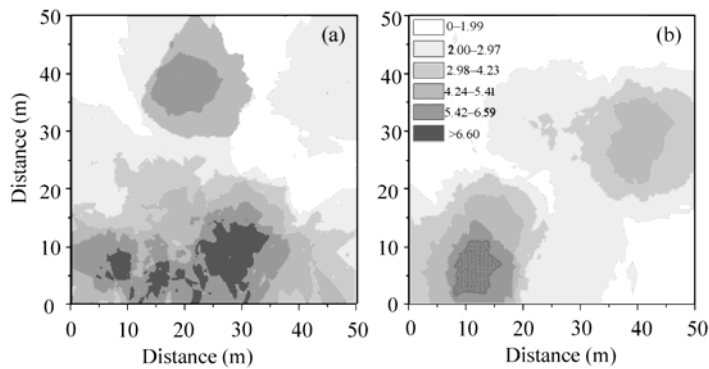


Fig. 4 Kriging interpolation analysis of individual CI (competition index) (a, Plot 1; b, Plot 2)

platyphylla and *P. davidiana* could produce a large number of winged seeds, which exhibited strong dispersion ability. Thus, they had no significant self-correlations at all spatial scales. Interspecies correlation analysis (Fig. 6) revealed that *Q. wutaishanica* was negatively correlated with *B. platyphylla* and *P. tabulaeformis* at small spatial scales, whereas no significant correlations were observed at large spatial scales and among other studied species. The result suggested that clumped *Q. wutaishanica* limited the recruitment of *B. platyphylla* and *P. tabulaeformis* at small-scales. We divided the trees into three classes based on the sizes (i.e., DBH), i.e., small trees (S, $DBH < 15$ cm), middle trees (M, $15 \text{ cm} \leq DBH < 25$ cm) and adult (large) trees (A, $DBH \geq 25$ cm). The spatial relationships of intraspecies competition based on different sizes of oak trees were then analyzed using univariate and bivariate O-ring statistics for the two development stages.

In the early development stage, clumped distribution of small and middle trees was found (Figs. 7 a–c). However, due to the lack of adult (large) and middle oak trees, self-correlation of adult trees and the spatial relationships of intraspecies competition were meaningless (Figs. 7d–f).

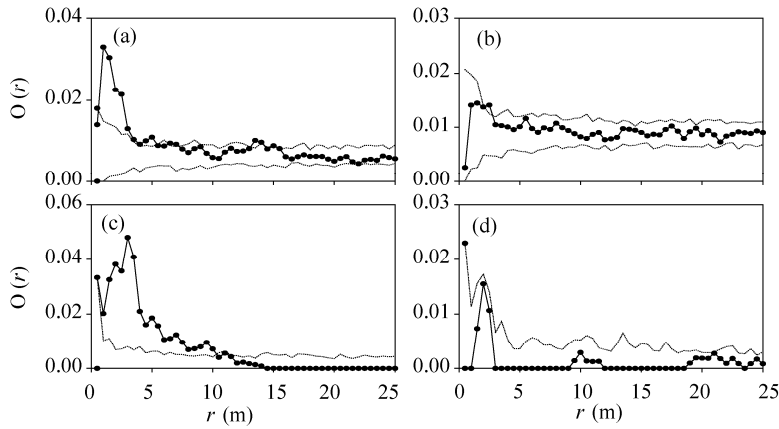


Fig. 5 Spatial relationships in intraspecies competition by univariate O-ring statistics ($O(r)$) of main tree species in the early development stage (a, *Quercus wutaishanica*; b, *Betula platyphylla*; c, *Pinus tabulaeformis*; d, *Populus davidiana*)

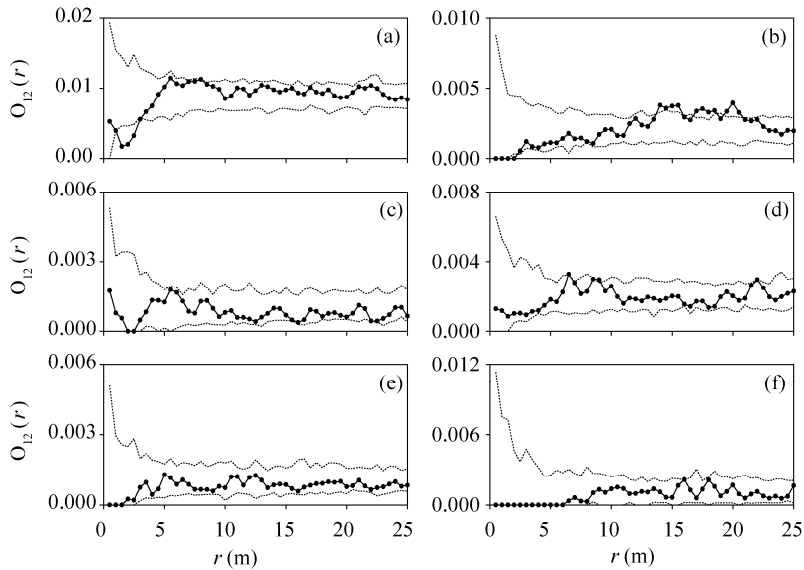


Fig. 6 Spatial relationships in interspecies competition by bivariate O-ring statistics ($O_{12}(r)$) in the early development stage (a, *Quercus wutaishanica*–*Betula platyphylla*; b, *Quercus wutaishanica*–*Pinus tabulaeformis*; c, *Quercus wutaishanica*–*Populus davidiana*; d, *Betula platyphylla*–*Pinus tabulaeformis*; e, *Betula platyphylla*–*Populus davidiana*; f, *Pinus tabulaeformis*–*Populus davidiana*)

However, in the late development stage, small oak trees showed positive spatial self-correlations at scales of 2–5 m (Fig. 8a). No obvious self-correlations were found between middle trees and adult (large) trees (Figs. 8b and c). Negative correlation was found between adult (large) and middle trees and also between adult (large) and small trees (Figs. 8d and e), and a weak positive correlation was found between middle and small trees at small spatial scales (Fig. 8f). It implied that smaller trees were impeded by the surrounding larger trees. Correspondingly, interspecies competitions were replaced by intraspecific competition from different sizes in late development stage.

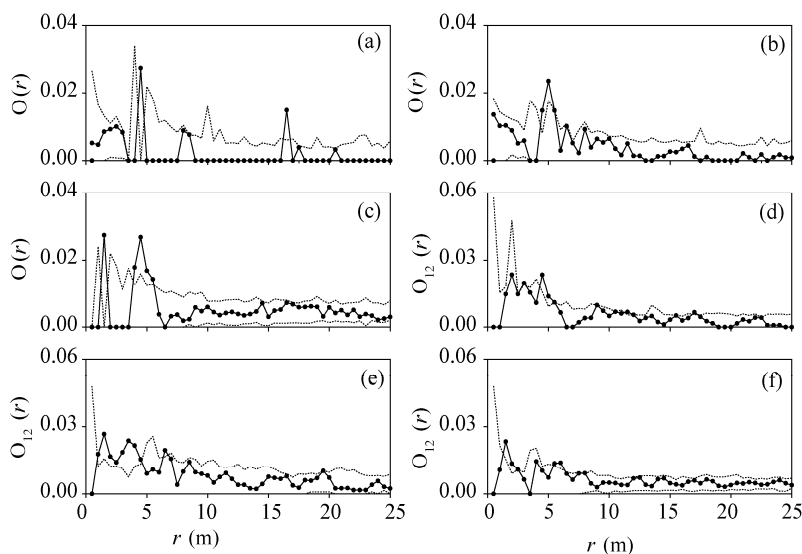


Fig. 7 Intraspecies spatial relationships between different sizes of oak trees in the early development stage based on univariate ($O(r)$) and bivariate ($O_{12}(r)$) O-ring statistics (a, adult trees; b, middle trees; c, small trees; d, adult–middle trees; e, adult–small trees; f, middle–small trees)

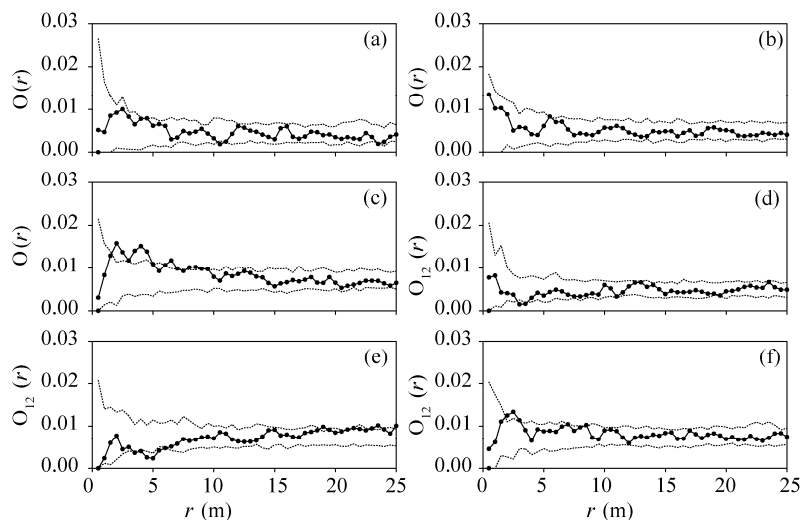


Fig. 8 Intraspecies spatial relationships between different sizes of oak trees in late development stage based on univariate ($O(r)$) and bivariate ($O_{12}(r)$) O-ring statistics (a, adult trees; b, middle trees; c, small trees; d, adult–middle trees; e, adult–small trees; f, middle–small trees)

4 Discussion

We found a positive self-correlation and high intensity of competition in *Q. wutaishanica* and *P. tabulaeformis*. These findings can be attributed to the biological characteristics of these tree species. That is, the heavy seeds of *Q. wutaishanica* and *P. tabulaeformis* clumped at small spatial scales, and the clumped seeds resulted in an intensive competition. By contrast, white birch (*Betula platyphylla*) produces a large number of winged seeds that can be dispersed readily by airflow. In addition, birch seeds tend to sprout in areas where competition is weak (Zhang et al., 2010; Gao et al., 2011). Our results further confirmed the early findings that birch trees were not strong competitors in oak forests.

Our study showed that the competition index (CI) expressing the competition intensity was negatively correlated with the sizes (DBH) of all tree species and the dependency of the competition intensity on the size (DBH) became weaker at the late development stage (see Fig. 3).

This finding is consistent with those by Tilman (1994) and Pedersen et al. (2012) who found that the competition intensity generally decreased with the growth of trees. At the early development stage of oak forests, oak and pine trees had high competition intensities (see Fig. 4a), suggesting that interspecies competition may have played an important role in the spatial distribution of tree species. Oak has a relatively high tolerance towards droughts and shades, promoting its dispersal in less habitable areas and thus becoming pioneer species on the CLP. In comparison, birch and aspen trees have narrow crowns and high intraspecies competition due to their clumped seedlings at small-scales. This finding is in agreement with that by Petritan et al. (2014) who found the same patterns in an old growth stage of *Quercus petraea*–*Fagus sylvatica* forest in western Romania. Again, the interspecies competition decreased at the late development stages primarily due to failures of those weak competitors (see Fig. 4b). Our finding that a forest tended to be homogenized in the late succession stage in terms of its species composition is quite similar with those reported by others (e.g., Barot et al., 1999; Getzin et al., 2006).

It should be mentioned that light was reported to have played an important role in interspecies competition. For example, Rees and Bergelson (1997) and del Río et al. (2014) suggested that asymmetric light competition might have resulted in different outcomes of interspecies competition. It means that the canopies of taller tree species may overshadow those of shorter tree species, thus resulting in stronger competitions of taller oak and pine trees and weaker competitions of shorter white birch and aspen trees (Qin et al., 2006; Su et al., 2009; Shao et al., 2012). It is our regret that we were not able to examine the relationship between light and interspecies competition simply due to our failure in finding a feasible method to accurately measure the crown width.

5 Conclusions

The spatial patterns and interspecies relationships of dominant species in mixed forests determine the community dynamics. This research found that intensive interspecies competition drove the diffusion of successor species (such as the oak trees on the CLP) and the successful diffusion was partially resulted from the failure of pioneer species in the interspecies competition during the early stages. After the invasive species replaced the pioneer species in some areas, interspecies competition drove the decreasing of the replaced population. In short, competition led to a reshaping of population structure, and even drove further changes of spatial patterns.

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