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# Local neighborhood competition following an extraordinary snow break event: implications for tree-individual growth

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**Sustainable forest management practices and the increased interest of plantation forestry in species mixtures require an understanding of individual-tree growth in complex and diverse forests. Individual-tree growth has been found to be affected by factors such as species identity and size of the target tree as well as of neighboring trees, neighbor density and abiotic factors. However, most of these studies have been conducted in plantations or mixed forests with a very limited number of species. We conducted our study in a subtropical forest in China, which was very species rich and highly heterogeneous with regard to topography (slope inclination and aspect, elevation) and successional status. Prior to our study the forest was subjected to an exceptional snow break event. We asked whether individual-tree basal area increment (BAI) over three growing seasons following the snow break event was related to local biotic and abiotic conditions. We hypothesized that individual-tree BAI is negatively affected by local neighborhood competition, positively affected by local neighborhood diversity, negatively related to slope inclination, and positively related to aspect to south. Individual-tree BAI of four different species was mainly affected by tree size, local neighborhood competition and species identity. Contrary to our expectations, we did not observe significant effects of local neighborhood functional diversity and abiotic conditions. However, we did find a negative effect of plot functional diversity on BAI. This finding may be explained by a negative correlation of plot functional diversity and snow break damage, which was observed in mid- and late-successional stages. The disturbance event did considerably change the competitive local neighborhood interactions by reducing competition, which increased the BAI of target trees in more disturbed/more diverse plots.**

**Keywords: Basal Area Increment, Crown Projection Area, Functional Diversity, Gutianshan National Nature Reserve, Local Neighborhood Diversity**

## Introduction

The increasing interest in sustainable forestry necessitates studies of structurally complex and diverse forests in order to understand their ecological processes and to integrate this knowledge in management approaches such as "close to nature" or mixed-species plantation forestry (Kelty 2006, Bauhus et al. 2009). In even-aged, simply structured monocultures, stand-based approaches are appropriate to explain and model tree growth. However, in structurally complex forest stands with a heterogeneous mixture of species, tree growth is strongly affected by intrinsic properties of individual trees and their local neighborhood (Canham et al. 2004, D'Amato & Puettmann 2004, Zhao et al. 2004). Accordingly, individual-tree approaches are much more appropriate than stand-based approaches for growth analyses, and individual-tree growth should be analyzed as a function of tree size, tree vitality, genotype, local neighborhood interactions, and local abiotic site conditions (Pretzsch 2009, Lang et al. 2010, Von Oheimb et al. 2011).

The local neighborhood conditions generally include biotic and abiotic factors. Among the most important biotic factors are tree-tree interactions. These local neighborhood interactions may occur as competition, but also as competitive reduction and facilitation (*i.e.*, complementarity - Kelty 1992, Forrester et al. 2006). These interactions have been modeled as a function of the size, number, and identity of tree individuals. Negative effects on the growth of a target tree have been observed where neighboring trees were larger, denser, or closer. Specifically, since competition for light is known to be size-asymmetric, larger individuals have a disproportionate effect on smaller individuals by shading (Schwinning & Weiner 1998). Distance-dependent competition indexes account for the distance between neighboring tree individuals, for their density as well as for their size ratios (Biging & Dobbertin 1992, Castagneri et al. 2008).

In mixed-species stands non-equivalent neighbor effects on individual-tree growth may not only be generated by distance and size ratios, but tree species may also differ in their competitive effects. It has been found that conspecifics are stronger competitors than heterospecifics (Stoll & Newbery 2005, Massey et al. 2006, Pretzsch & Schütze 2009, Von Oheimb et al. 2011). This may be due to high competitive equivalence between individuals of the same species, whereas individuals of different species may use resources in a complementary, and thus more efficient way, and, thereby, reduce competition. At the stand level a positive effect of diversity on tree growth has been confirmed for forest systems of different biomes such as the neotropics (Ruiz-Jaen & Potvin 2010), the Mediterranean region (Vila et al. 2007) as well as the temperate and boreal zone (Paquette & Messier 2011). Following the local neighborhood approach we expect that local diversity should positively affect individual-tree growth as well. However, this has rarely been studied for highly diverse and structurally complex (near-) natural forest ecosystems.

Furthermore, the effects of abiotic factors have to be included in individual-tree growth analyses, because resource availability is not only determined by the local biotic, but also by the local abiotic conditions. On sloping terrain, for example, topography (*i.e.*, slope

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inclination and aspect) is one of the major factors influencing solar irradiation, temperature and soil moisture availability (Ishii & Higashi 1997, Warren 2010).

Finally, tree growth analyses have to consider that growth rates vary through time as a response to changes in environmental conditions (*e.g.*, climate) and local neighborhood interactions, but also as a result of natural or human disturbances. These disturbances selectively remove or kill neighbors from the local environment of residual trees and can, therefore, influence interactions among individuals and the local environment-growth relationship (Hartmann & Messier 2011). Important types of natural disturbances are snow and ice storms (Bragg et al. 2003). The resulting tree damages, such as breakage of stems or crown, cause shifts of the light regime of the forest stand, predominantly towards an increased spatial heterogeneity. Damaged tree individuals have been shown to have lower increases in stem diameter than their undisturbed neighbors (Smolnik et al. 2006, Aubrey et al. 2007). The growth reduction in turn has implications for local neighborhood interactions since this affects the competitive strength of tree individuals.

The aim of the present study was to predict individual-tree growth in a heterogeneous mixed forest stand by means of biotic and abiotic factors of the local neighborhood. The study was conducted in a subtropical broad-leaved evergreen forest in China. China aims at sustainable forest management and large areas have been afforested (Zhang & Song 2006, Cao et al. 2011). However, afforestations are mostly monocultures causing a variety of environmental problems (Cao et al. 2008, 2011).

The studied forest is very species-rich and heterogeneous with regard to topography (slope inclination and aspect) and successional stages. Prior to our study the forest area experienced an exceptional snow break event. In this complex forest stand we wanted to know if individual-tree basal area increment (BAI) over three growing seasons following the snow break event is related to local biotic and abiotic conditions. More precisely we hypothesized:

- (H1): Individual-tree BAI is negatively affected by local neighborhood competition.
- (H2): Individual-tree BAI is positively affected by local neighborhood diversity.
- (H3): Individual-tree BAI is negatively related to slope inclination.
- (H4): Individual-tree BAI is positively related to aspect to south.

## Material and Methods

### Study site

The study was conducted in the Gutianshan National Nature Reserve (NNR), which is located in Zhejiang province, P.R. China (29º 8.18 - 29º 17.29 N, 118º 2.14 - 118º 11.12 E). The Gutianshan NNR has an area of about 81 km$^2$ with elevations ranging from 250 to 1250 m a.s.l. It is situated in the subtropics with a warm temperate climate and a short dry season in winter. The mean annual temperature is 15.1 °C and the mean annual precipitation is about 1964 mm (Hu & Yu 2008).

The potential natural vegetation is subtropical broad-leaved evergreen forest, with a similar number of coexisting evergreen and deciduous broad-leaved species, though evergreen species is dominating in abundance (Hu & Yu 2008). The forest is species-rich as 59 woody species > 1m height have been identified on a plot of 30 x 30 m size (Bruelheide et al. 2011). The area is heterogeneous with respect to the successional stages, with older stands dominated by *Castanopsis eyrei* (Champ. ex Benth.) Hutch. and *Schima superba* Gardn. et Champ. and younger dominated by *Pinus massoniana* Lamb. and *Quercus serrata* Murray var. *brevipetiolata*. Our study sites comprise intermediate to steep slopes (ranging from 10° to more than 50°) and small-scale changes of aspect. The study area was affected by an extraordinary snow break event in January/February 2008 (Zhou et al. 2011) with many trees exhibiting stem breakage or crown loss of differing extent (Man et al. 2011).

### Study design

Field data have been collected in autumn of 2008 and 2011 on 27 plots of 30 x 30 m size within the framework of the BEF (Biodiversity and Ecosystem Functioning) China project. The plots were randomly chosen within the Gutianshan NNR (limited by inaccessibility and avoiding areas of high snow break damage) and stratified by successional stage: (1) <20 yrs; (2) <40 yrs; (3) <60 yrs; (4) <80 yrs; (5) ≥80 yrs (Bruelheide et al. 2011). The elevation of plot locations ranged from 250 to 900 m.

We selected four target species of high abundance (Yu et al. 2001): *Castanea henryi* (Skan) Rehd. et Wills. and *Q. serrata* var. *brevipetiolata* (both deciduous), *C. eyrei* and *S. superba* (both evergreen). Within the plots 20 target trees per species (10 for *C. henryi*) were chosen randomly from all individuals complying with the following criteria: (i) single stemmed; (ii) diameter at breast height (dbh, 1.3 m above ground) >10 cm (intermediate and old plots) or dbh >3 cm (in young plots); (iii) crown position in the upper canopy; (iv) no or only slight crown damage caused by the snow break event; (v) each target species could only be selected once per plot. Following the local neighborhood approach we assume that important interactions take place between neighboring tree individuals (Pretzsch 2009). Target tree neighbors were defined by using the reversed cone method following Biging & Dobbertin (1992) with an opening angle of 70° of the cone. This approach was used because in a native forest remnant of the same study region Von Oheimb et al. (2011) found that the mode of competition in this forest type is primarily size-asymmetric, *i.e.*, competition for light. For a tree on a slope, the crowns of neighboring trees in an uphill direction are situated at a higher position than those of the same-sized neighbors in a downhill direction and may, thus, impose a stronger influence on individual-tree growth at a given height. The search cone method takes this into account by giving more weight to tree height than distance: more neighbors are included in uphill than in downhill direction at a given opening angle. Each target tree together with its neighbors formed a target group. For a more detailed description we refer to Lang et al. (2010).

### Field data

We measured the dbh of all target trees in 2008 and 2011 by means of a diameter measurement tape. The measurement positions on the trees were permanently marked with white color. Radial increment was calculated as basal area increment per year (BAI in cm$^2$ yr$^{-1}$). The relative position of the neighbors to the target tree was determined by recording the azimuth and horizontal distance from stem base to stem base. For all individuals eight crown radii in the cardinal and ordinal directions were measured, each being the distance, determined by means of a densiometer, from crowntip to the stem. Crown projection areas (CPA) of all tree individuals were calculated as polygons based on the eight radii. Crown measurements took place in 2008 and 2011. The horizontal distances of all neighboring trees to their target tree and the crown radii were measured using a Forester Vertex Hypsometer (Haglöf, Sweden).

To describe the local competition experienced by each target tree, we used a distance dependent competition index (CI) modified after Castagneri et al. (2008), with the CPAs to describe the size of tree individuals (eqn. 1):

$$CI=\sum_{j=1}^{n}\frac{(CPA_j/CPA_t)^2}{(dist_{tj}+1)}$$

where $CPA_j$ is the neighbor tree crown projection area (m$^2$); $CPA_t$ is the target tree crown projection area (m$^2$); $dist_{tj}$ is the horizontal distance (m) between the neighbor *j* and the target tree *t*.

Two competition indexes were calculated. One was based on CPAs of 2008 ($CI_{08}$) and refers to the situation immediately after the snow break event. The other competition index was based on CPA measurements of

**Tab. 1** - Comparison of the most parsimonous models explaining BAI, original full models have been fitted with competition based on crown data of 2008 (Model A) and based on crown data of 2011 (Model B).

| Model | Parameters | DF | F-value | P-value |
|---|---|---|---|---|
| Model A | Initial dbh | 35 | 16.24 | <0.001 |
| | Species identity | 35 | 3.8 | 0.011 |
| Model B | Initial dbh | 34 | 17.72 | <0.001 |
| | Competition | 34 | 5.97 | 0.021 |
| | Plot functional diversity | 25 | 5.39 | 0.021 |
| | Species identity | 34 | 2.88 | 0.037 |

2011 (CI$_{11}$), thus including the growth reactions of crowns three growing seasons after the disturbance event.

Local and plot functional diversity was calculated as Rao's quadratic entropy (Rao's Q - Rao 1982, Botta-Dukat 2005) of eight functional leaf traits (these were specific leaf area; leaf dry matter content; content of nitrogen, aluminium, calcium and phosphorus; C/N ratio; stomata density) of either all neighboring trees of a target group (local functional diversity) or all individuals >1 m height of the plot (plot functional diversity, for trait data description see Kröber et al. 2012). A detailed description of the calculation of Rao's Q is provided by Lang et al. (2012b).

Furthermore, the local environmental parameters slope inclination and aspect and plot elevation a.s.l. were recorded. To quantify the severity of disturbance of the snow break event we first estimated the percentage of crown loss of former undisturbed crowns of each tree individual. Categories were defined as undamaged (0% loss) = 0, 1-25% loss = 1, …, crown completely broken 100% loss = 5. Plot level disturbance was then calculated as the summed mean category scores of all individuals divided by the number of observed individuals.

### *Statistical analyses*

A total of 65 target trees entered the analyses. Between 2008 and 2011 one plot with two target trees was destroyed. Two of the small diameter target trees (10 cm and 11 cm dbh, respectively) showed the highest absolute BAIs, and the target tree with the largest dbh (56 cm in 2008) had an extremely low BAI. These five target trees were excluded from the analyses, resulting in 10 target trees of *C. henryi*, 19 target trees of *C. eyrei*, 18 target trees of *Q. serrata* and 18 target trees of *S. superba* which have been analyzed.

We tested the effects of the initial dbh, environmental parameters (slope inclination and aspect, elevation, damage caused by the snow break event), local neighborhood competition, local neighborhood and plot diversity and species identity on the BAI of target trees. Two full linear mixed effects models were compared with regard to the competition indexes used: CI$_{08}$ *vs.* CI$_{11}$. Plot was fitted as a random factor of the mixed effects models to account for the spatial nesting of data, namely the blocking of target groups within plots. Model simplification was done by stepwise backward selection of fixed factors, removing the least significant variables until only significant predictor variables were left ($p < 0.05$).

The response variable was square root transformed to meet the criterion of normality. Prior to the analyses, all predictor variables have been checked for collinearity (correlations between variables did not exceed R = 0.6) and all numerical variables have been centered and scaled to ensure comparability of results. We assessed by plotting that residuals were well behaved, that the response variable is a reasonable linear function of the fitted values and that errors are normally distributed within the plots (Crawley 2007).

Differences in crown loss due to the snow break event between plots of different successional stages were assessed by ANOVA. The relation between plot functional diversity and crown loss of older plots (successional stages 3-5) was analyzed by a linear model.

All statistical analyses were performed using R 2.15.3. Linear mixed effects models were analyzed by means of the package "nlme" (Pinheiro et al. 2010) and multiple comparisons were performed using the package "multcomp" (Hothorn et al. 2008).

## Results

The variability in target tree BAI was mainly explained by initial dbh (effect size: 0.34, model A and 0.42, model B - Tab. 1). The thicker the stem of an individual-tree, the higher was its BAI. Furthermore, BAI was significantly different between the tree species. With a mean initial diameter of 18 cm BAI amounted to 12.1 ± 0.1 cm$^2$ yr$^{-1}$ in *C. henryi*, to 9.0 ± 0.1 cm$^2$ yr$^{-1}$ in *C. eyrei*, to 7.0 ± 0.1 cm$^2$ yr$^{-1}$ in *S. superba* and to 4.6 ± 0.1 cm$^2$ yr$^{-1}$ in *Q. serrata,* as calculated from species-specific regressions (for observed means see Fig. 1). The BAI of *Q. serrata* was significantly lower than those of the other species (post-hoc Tukey Test, $p < 0.05$).

Although our study area was highly variable with regard to topography, neither slope inclination and aspect nor elevation was included among the significant predictors in the final models. Likewise, we did not find an effect of snow damage on target tree BAI.

The competitive strength of neighboring trees, expressed as CI$_{11}$, negatively affected BAI (effect size: -0.19 - Tab. 1). However, only CI$_{11}$ could be retained in the final model, whereas CI$_{08}$ had no predictive power. This was further confirmed by a comparison of the two models containing initial dbh, CI$_{08}$ (model 1) or CI$_{11}$ (model 2), plot functional diversity and species identity (Akaike's Information Criterion - AIC: 166.15 *vs.* 165.89).

Local functional diversity had no predictive power, whereas plot functional diversity was retained in the final model with CI$_{11}$ (Tab. 1). Plot functional diversity negatively affected BAI and had a similar effect size as

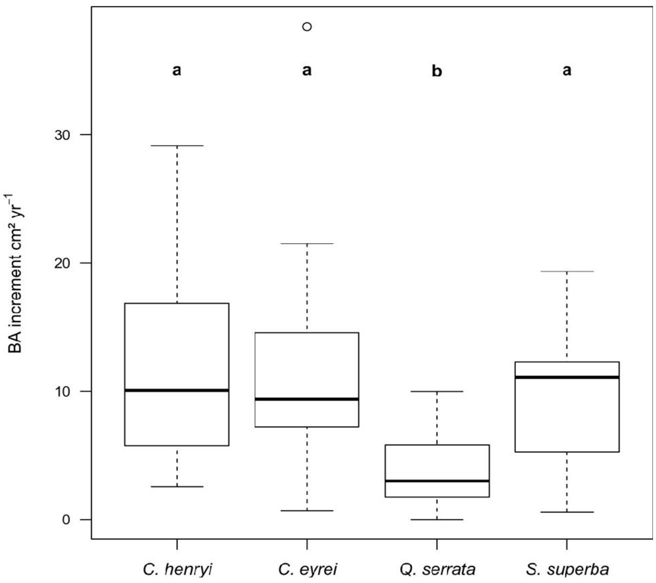

**Fig. 1** - Boxplots of BAI of target species. Different characters denote significant differences.

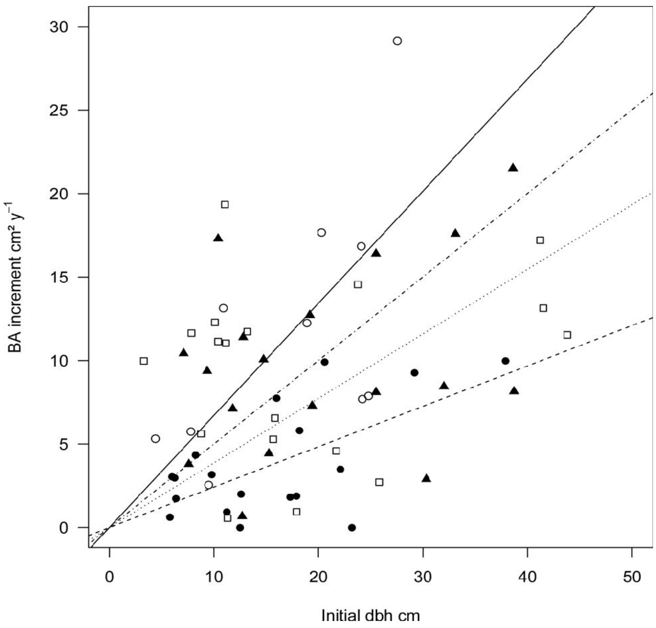

**Fig. 2** - Linear regressions of BAI over initial dbh (2008) for each target species. Open circles; unbroken line: *C. henryi*; triangles; dotdashed line: *C. eyrei*; bullets; dashed line: *Q. serrata*; quadrats; dotted line: *S. superba*.

$CI_{11}$ (effect size: -0.25).

When comparing the damage due to snow break between plots of different successional stages, we found that only plots of the intermediate and late stages have been affected (ANOVA: F-value = 100.1; p < 0.001). Young stages did not show any damage at all (Fig. 3). Using the plots of the intermediate and late stages we found that the degree of disturbance by snow break was significantly less in plots of higher functional diversity (linear model: estimate = -0.43; p < 0.001 - Fig. 3).

## Discussion

This study provided evidence that in heterogeneous species-rich forests BAI of target trees of four species was mainly determined by tree size, local neighborhood competition and species identity. Surprisingly, we found no effect of local neighborhood functional diversity but a negative effect of plot functional diversity on BAI. For plots of mid- and late-successional stages this may be explained by the stronger snow break damage with higher plot functional diversity.

Our models showed that the initial dbh had a strong positive effect on BAI. This is in accordance with other studies, which emphasize the importance of size factors in predicting individual-tree radial growth (Stoll et al. 1994, Crescente-Campo et al. 2012, Bowman et al. 2013). However, there is considerable variation in the diameter-BAI relationship, as displayed in Fig. 2. In a natural mixed-species and multi-age forest the diameter-BAI relationship is obscured by the coexistence of slow-growing older trees and fast-growing younger ones (Bowman et al. 2013). Additionally, species-specific differences in BAI contribute to this finding. These differences indicate that there is interspecific variation in functional traits between the four tree species. For three of the four species Lang et al. (2012a) found species-specific differences in sapling growth in the same study region. Furthermore, Chen et al. (1999) observed high growth rates for saplings of *S. superba* in forest gaps, and *Q. serrata* was recorded to be very slow growing (Xing et al. 2012). However, further studies are needed to elucidate the relationships between functional traits and growth rates in these subtropical forests.

Topography (*i.e.*, slope inclination and aspect) has important implications for the direction and intensity of incoming radiation (Ishii & Higashi 1997). In the northern hemisphere, south-facing slopes receive much more solar irradiation than north-facing slopes, creating strong gradients of light, temperature and soil moisture: higher light levels and temperatures as well as lower soil moisture corresponds with south-facing slopes. Furthermore, slope inclination may correlate with edaphic conditions, in particular soil depth, soil moisture and nutrient availability. Steeper slopes may be shallower, and therefore may limit rooting space in one dimension. Slope inclination has been shown to affect the stature of a tree in terms of stem inclination and crown asymmetry (Umeki 1995, Lang et al. 2010). Contrary to our third and fourth hypothesis, however, topography had no effect on BAI in our study. High morphological plasticity of the target species may be the reason for the low sensibility of radial growth towards topographic conditions in these highly variable environments (Lang et al. 2010).

### *Competition*

The results of our study confirm our first hypothesis. Local neighborhood competition

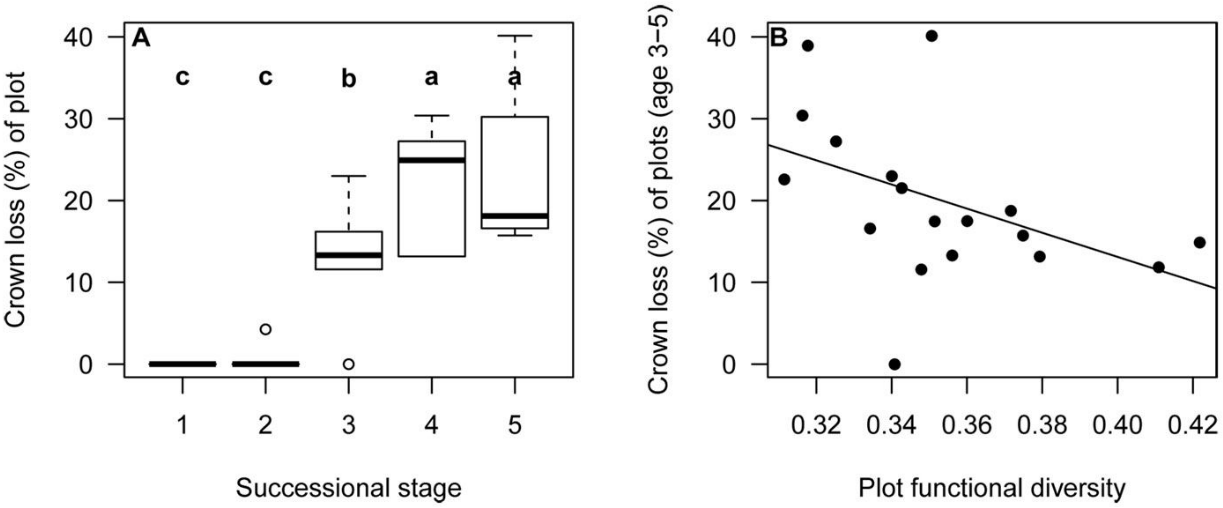

**Fig. 3** - Percentage of crown loss due to a snow break event per plot for different successional stages (A) and correlation of crown loss of older plots and plot functional diversity (B). Different characters denote significant differences.

(expressed as $CI_{11}$) was an important predictor of individual-tree BAI. We calculated the CI with tree data from two different points in time, but, interestingly, we found that only $CI_{11}$ was significantly related to BAI, whereas $CI_{08}$ was not. Furthermore, the full model 2 including $CI_{11}$ had stronger predictive power than the full model 1 in which $CI_{08}$ was included. $CI_{08}$ was calculated based on the conditions directly after the snow break event, but did not contribute to explain the variability in BAI over the three growing seasons following this event. The extreme snow break event of January 2008 is clearly an important natural disturbance of these subtropical forests, occurring with a mean frequency of 50 to 100 years (Shao et al. 2011). When establishing the permanent plots in summer 2008, we selected plots with comparatively low damage by the snow storm. Nevertheless, our results show that this rare disturbance event reduced competition also in the less damaged forest patches, which may considerably change the competitive interactions.

### *Diversity*

In contrast to our second hypothesis, we did not find any effect of local neighborhood functional diversity on BAI. There might be two possible explanations for this finding. Firstly, it has been found that complementary effects vary over time, with stand development and local neighborhood species composition (Boivin et al. 2010, Cavard et al. 2011, Forrester et al. 2011). Since this is an observational study we could not strictly control the different factors. Future research in a newly established large-scale forest BEF experiment of the BEF-China project is designed to systematically analyze species interactions under controlled conditions (Yang et al. 2013). Secondly, the disturbance caused by the snow break event had a strong effect on local neighborhood interactions. These effects may have overruled local diversity effects. Future investigations of the local neighborhood interactions in the permanent study plots will elucidate whether there is a longer term influence of the snow break event on tree growth.

Surprisingly, we did find a negative effect of plot functional diversity on BAI. We suspect that this is not a direct effect. We found that young plots did not suffer from damage caused by snow break. This is in general accordance with Man et al. (2011) who observed the largest proportion of undamaged trees in the lowest dbh class included in their study in the Gutianshan NNR (*i.e.*, 8 - 10 cm). Small trees are presumably less prone to snow break damage due to their relatively smoothness of stems and restricted CPA. Including only plots from intermediate and late successional stages we found that snow break was reduced in plots of higher functional diversity (Fig. 3). Thus, we hypothesize that a higher crown loss in less diverse plots, increased incoming sunlight and canopy space, for enhancing individual-tree growth. In our study sites, Lang et al. (2012b) found that higher plot functional diversity was correlated with higher horizontal heterogeneity of the canopy. Furthermore individual tree CPA has been found to increase with local functional diversity (Lang et al. 2010). Thus, the heterogeneous light conditions in more diverse stands may promote optimal crown growth and stability, leading to a decrease of snow break damage.

## Conclusions

The pronounced differences between $CI_{08}$ and $CI_{11}$ point to the relevance of multiple assessment of competition in time (Hartmann & Messier 2011). We conclude that the influence of snow break on local neighborhood interactions, rather than the direct effect of the event, affected the growth response of surviving trees. These strong effects may impact stand structure and dynamics in the long run. Thus, we may ask if in future the disturbances of these extreme weather events, even more than today, may represent the main driver of forest growth and structure.

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