Mechanisms promoting tree species co-existence: Experimental evidence with saplings of subtropical forest ecosystems of China

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biomass allocation; branch demography; complementarity; crown architecture; density; facilitation; niche differentiation; species composition; species identity; species richness

Nomenclature
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Conclusions: Effects of species composition and species identity on growth rates and crown architecture variables of tree saplings point to niche separation as a mechanism of species co-existence, while effects of species richness were not yet prominent at the sapling life stage.

Introduction
The question as to which mechanisms maintain and promote species co-existence has become increasingly important in light of biodiversity loss and species extinction (Barot 2004; Hillebrand & Matthiessen 2009). Two theories play a key role in the current discussion on plant species co-existence: neutral theory and niche theory. According to neutral theory, functional equivalence (i.e. co-occurring species do not have to be different in rates of growth, dispersal or speciation), together with stochastic events, is a sufficient explanation for species co-existence.
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(Hubbell 2005; Rosindell et al. 2011). Niche theory, by contrast, implies that co-existence is explained by inter-specific differentiation in response to exploitative competition for environmentally limiting resources (DeClerck et al. 2005; Kraft et al. 2008) or in response to species-specific pathogens (Petermann et al. 2008; more general: Loreau & Hector 2001; Silvertown 2004; Levine & HilleRisLambers 2009). Niche partitioning may occur in space, in time or with regard to the quality of resources. As a result, in species combinations resources may be used in a complementary and more efficient way than in monocultures, and inter-specific competition is reduced compared to intra-specific competition (Kahmen et al. 2006).

For trees, the most important above-ground resource is light (Denslow 1987; Canham et al. 1994). Since light-harvesting efficiency is significantly affected by biomass allocation to leaves, foliage distribution and branching frequency (Niinemets 2010), the separation in niche space with regard to light harvesting should be evidenced by species-specific growth patterns, biomass allocation or plant architecture. In addition to abiotic factors, competitive interactions strongly influence individual tree growth. In particular, crown dimensions and architecture are known to respond sensitively to local neighbourhood interactions (Biging & Dobbertin 1992; Getzin et al. 2008; Schrötter et al. 2011). However, to explain the spatial development of crowns in detail, information on single branches of individual trees is needed, since the process of crown expansion depends on the spatial development of branches and branch demography, which in turn is affected by local neighbourhood interactions (Franco 1986; Stoll & Schmid 1998; Sumida et al. 2002).

In this study, we experimentally analyse mechanisms of species co-existence of individual trees at the sapling stage, making use of the local neighbourhood approach (Pretzsch 2009). The maintenance of a diverse sapling pool is important to ensure the regeneration and persistence of species-rich forests (Bruelheide et al. 2011). In particular, crown dimensions and architecture are known to respond sensitively to local neighbourhood interactions (Biging & Dobbertin 1992; Getzin et al. 2008; Schrötter et al. 2011). However, to explain the spatial development of crowns in detail, information on single branches of individual trees is needed, since the process of crown expansion depends on the spatial development of branches and branch demography, which in turn is affected by local neighbourhood interactions (Franco 1986; Stoll & Schmid 1998; Sumida et al. 2002).

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We planted saplings of four early-successional subtropical species in monoculture as well as in two- and four-species combinations. In order to determine whether niche separation is the mechanism that enables the co-existence of these species in an early stage of their life, we tested for species richness, species composition and species identity, as well as for density and initial diameter size effects. Specifically, we tested the following hypotheses:

(H1) Species richness of the local neighbourhood affects the growth and morphology of saplings.
(H2) Species composition of the local neighbourhood affects growth and morphology of saplings.
(H3) Species identity of the target sapling is an important predictor of its growth and morphology.
(H4) Density affects growth and morphology of saplings.

Methods

Study area and experimental design

Our experiment was set up near Xingangshan, Jiangxi Province, southeast China (29°06′33″N, 117°55′24″E). The study area is characterized by a subtropical monsoon climate with an average annual precipitation of approximately 2000 mm and a mean temperature of 15.1 °C. The natural vegetation is a subtropical broad-leaved forest with dominance in abundance of evergreen species (Bruelheide et al. 2011). Nevertheless, the number of occurring deciduous and evergreen species is almost balanced (Lou & Jin 2000). The subtropical broad-leaved forest ecosystems of southeast China represent a global hotspot of phytodiversity (Barthlott et al. 2005).

The experimental area was a former agricultural field, which was ploughed, harrowed and divided into four blocks prior to setting up the experiment in March 2009. Four highly abundant, early-successional species were chosen for the experiment: Schima superba Gardn. et Champ., Elaeocarpus decipiens Hemsley (evergreen), Quercus serrata Murray and Castanea henryi (Skan) Rehd. et Wils. (deciduous) (Yu et al. 2001). We manipulated species richness and species composition of tree saplings on plots of 1 m² in size. Three plot-related species richness levels were established: monocultures, two-species combinations and four-species combinations. The four monocultures of each species, all six possible two-species combinations, and one four-species combination made a total of 11 species compositions. In addition to enabling analysis of species richness effects, the comparison of all possible species combinations also makes it possible to identify the effects of intra-specific vs. inter-specific competition (Massey et al. 2006), as well as competitive dominance of specific species. Species identity was treated as another predictor variable in the experiment. Finally, the species richness and species composition treatments were fully crossed with a density treatment. The low-density
treatment comprised only one individual per plot, whereas the experimental plots with high and intermediate density each contained 16 individuals, planted in an array of four by four. Planting distances between saplings in the high- and intermediate-density treatment were 15 and 25 cm, respectively. The high, intermediate and low densities in this experiment refer to 44 000, 25 000 and 10 000 saplings per ha, respectively. In the nearby Gutianshan Nature Reserve, densities of 16 000 individuals per ha were found in an early successional secondary forest stand (<20 yr; Bruelheide et al. 2011). In the species combinations, each species was represented by the same number of individuals in both the peripheral rows (i.e. 12 individuals) as well as in the centre (i.e. four individuals). To avoid edge effects, all analyses were performed using the four central individuals. All treatment combinations were replicated four times, once in each of the four blocks. The total number of plots was 132 (11 species compositions x two densities (high, intermediate) x four blocks + 11 low-density plots spread over four blocks x four species = 88 + 44 plots). All treatment combinations were randomly assigned to plots within blocks. The experiment was run until September 2010, when destructive harvest took place. Individuals of the intermediate density treatment of one block were harvested in July 2010.

Field measurements

Sapling mortality

Over the course of the experiment, 223 out of 1452 saplings died (15.4%; number of dead saplings per species: C. henryi 92, S. superba 95, Q. serrata 18, E. decipiens 18). Since 96% of these dead individuals died during the first growing season (March to October 2009), post-planting stress was assumed to be the main reason for sapling mortality. Consequently, only data of saplings that survived this phase of establishment were incorporated in the analyses.

Sapling growth

Total height of saplings (i.e. length from ground to apical meristem) was measured in November 2009 and September 2010. Stem diameter at base height was measured 5 cm above ground in N-S and E-W direction with calipers, and the mean value was used in the analyses. The position of the diameter measurements was marked permanently with white paint. Measurements were taken in March 2009 (initial stem diameter), November 2009 and September 2010. Growth rates of absolute height and diameter were calculated as: [value (September 2010) – value (November 2009)]/11.

Above-ground biomass

To analyse biomass allocation patterns with regard to stratification (i.e. height layers) and to different constituents (stem, branches and leaves), the four central individuals per plot were harvested in September 2010 in 50-cm strata starting from ground level. Saplings were divided into stem, branches and leaves for each stratum. Biomass was dried at 70 °C for 48 h and weighed to 0.01 g precision. Biomass data were logarithmically transformed prior to analyses.

To analyse the vertical above-ground biomass distribution, we calculated the cumulative biomass fraction C, i.e. the proportion of cumulative above-ground biomass, summed from ground level to the height strata $hs$ (50, 100, 150, 200, 250 cm). For each individual we fitted the coefficient of vertical biomass distribution as the linear regression coefficient $\beta$ of $C$ over $hs$ (see Jackson et al. 1996; Vonlanthen et al. 2010). The coefficient of vertical biomass distribution indicates the steepness of declining $C$ with increasing $hs$. Higher coefficient values, in turn, indicate biomass more evenly distributed over the total height of the tree.

Crown architecture

All crown architectural parameters were determined in June and September 2010. A branch was defined as a primary furcation longer than 1 cm. The height of the first branch was measured, and crown length was calculated as the difference between total sapling height and height of the first branch. The length of the first and the longest branch was measured as the distance from the stem to the longest tip of the respective branch.

Branch demography

Branches were counted bi-monthly during winter 2009/2010 (November, January, March) and monthly from April to June 2010 and in September 2010. Branch turnover and pruning are interpreted as a measure of adaption ability to changes in neighbourhood conditions over time. Branch turnover was calculated as the sum of all changes in branch number (no matter whether positive or negative) from November 2009 to June 2010. Pruning was defined as the sum of all negative changes in branch number (November 2009 to June 2010) and describes the dieoff of branches over time.

Statistical analyses

First, the complete data set was used to test for (H1) by fitting mixed effects models (Model 1) including species richness and density as factorial variables and the initial diameter as fixed effect. The initial diameter was used to
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account for differences in size at the beginning of the experiment. Second, all two-species combinations were analysed for species composition (H2). Mixed effects models (Model 2a) were fitted using species composition, density and initial diameter as fixed effects. The analyses with Model 2b were performed for the high-density treatment data divided by species to exclude density effects and to test for composition effects on the individual level of each species. Species composition in Model 2a referred to the mean over all individuals of a given species composition, whereas in Model 2b species composition referred to the mean of individuals of a specific species within a given species composition. Model 2b contained species composition and initial diameter as fixed effects. Third, mixed effects models (Model 3) for all monocultures were calculated to test (H3). They were fitted by the predictor variables species identity, density and initial diameter as fixed effects.

Random effects for all models were plot nested in block. Model simplification was performed by step-wise backward selection of fixed factors, removing the least significant variables until only significant predictory variables remained ($P < 0.05$). Since all density treatments were included in the analyses of Models 1, 2a and 3, the complete data from the June 2010 measurements was used to ensure a balanced data set. Model residuals did not show violation of modelling assumptions (normality and homogeneity of variances). The significant categorical variables were further examined by a Tukey post-hoc test. For the sake of clarity and more comprehensive analyses, the models presented here did not account for the presence and absence of species (for these models Appendix S1). We conducted a test for a phylogenetic signal (K statistics) in the observed growth and crown architectural traits. Although the K values for crown length and branch biomass were close to one, none of the values were significant, and we did not consider phylogeny in the statistical analyses (Appendix S2). In addition, we calculated Pearson correlation coefficients between height and diameter growth rates and crown architectural variables. If not indicated otherwise, values are given as mean with standard deviation.

All statistical analyses were performed using R 2.12. (R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria) using the packages nlme for the analyses of mixed effects models, multcomp for post-hoc Tukey tests and picante for the K statistics.

Results

Height and diameter increment

The mean sapling height at the time of planting was 33 cm ± 13 cm, compared to a mean height of 124 cm ± 39 cm at the end of the experiment. $S. superba$ ($6.74 \pm 2.17$ cm month$^{-1}$) had the highest mean absolute height growth rate, followed by $E. decipiens$ ($6.31 \pm 2.27$ cm month$^{-1}$), $Q. serrata$ ($5.57 \pm 2.34$ cm month$^{-1}$) and $C. henryi$ ($3.63 \pm 2.67$ cm month$^{-1}$). Species richness had no significant impact on the absolute height growth rate of saplings. However, species composition significantly affected absolute growth rates ($P = 0.03$). Model 2b revealed that the height growth rate of $C. henryi$ ($P = 0.019$) and $Q. serrata$ ($P = 0.046$) individuals was affected by species composition. Individuals of both species were significantly higher in combination with $E. decipiens$ compared to monocultures. The absolute height growth rate was also influenced by species identity ($P < 0.001$). Neither density nor the initial stem diameter of saplings affected height growth.

The mean absolute diameter growth rates per month were: $E. decipiens$ ($0.7 \pm 0.5$ mm) > $S. superba$ ($0.6 \pm 0.3$ mm) > $Q. serrata$ ($0.5 \pm 0.3$ mm) > $C. henryi$ ($0.3 \pm 0.3$ mm). Absolute diameter growth rates were neither affected by species richness nor by species composition. However, species identity was a highly significant predictor of diameter growth ($P = 0.008$). The diameter growth rate of $C. henryi$ was significantly lower than that of $S. superba$ and $E. decipiens$ ($P < 0.05$). In addition, density had a significant influence on absolute diameter growth rate ($P < 0.001$). The diameter growth of saplings was significantly enhanced in the low-density treatment compared to both the intermediate- and high-density treatment ($P < 0.001$). In contrast, the initial stem diameter had no significant effect on diamter growth.

Both absolute height and diameter growth rates were positively correlated with crown length (Pearson correlation coefficient, $r = 0.84/0.50$, respectively), the length of the longest branch ($r = 0.40/0.51$) and the number of branches ($r = 0.49/0.45$).

Above-ground biomass

Model 1 revealed no significant effect of species richness on above-ground biomass or on the coefficient of vertical biomass distribution. Species composition, in contrast, significantly influenced biomass increment ($P = 0.009$) and allocation to different constituents ($P < 0.01$). Results of Model 2b showed that $C. henryi$ individuals accumulated significantly more biomass in combination with $E. decipiens$ than in the monoculture ($P < 0.001$) and in combination with $S. superba$ ($P = 0.023$; Fig. 1a). The biomass of leaves of $C. henryi$ individuals was significantly lower in monocultures than in combination with $E. decipiens$ ($P = 0.005$) or in the four species combination ($P = 0.025$; Fig. 1b). Similar to $C. henryi$, the stem and total biomass of $Q. serrata$ individuals was higher in combination with $E. decipiens$ than in
monoculture ($P < 0.01$) and in combination with *C. henryi* ($P < 0.05$; Fig. 1c, d). Species identity was a significant predictor of all biomass-related variables (all $P < 0.001$). In general, results of post-hoc Tukey tests revealed that the biomass of all constituents of *C. henryi* was significantly lower than that of the other species (Table 1).

Stratum-related biomass allocation patterns of different constituents proved to be quite stable over density treatments for each species (Fig. 2). Species identity effects were evident for the coefficient of vertical biomass distribution ($P < 0.001$). Increasing density had negative effects on all biomass constituents ($P < 0.05$), whereas no density effects on the vertical biomass distribution were found. Regarding the total above-ground productivity within the low-density treatment, the four species ranked as follows:

- *S. superba* ($157.2 \pm 134.7$ g) > *E. decipiens* ($135.2 \pm 145.99$ g) > *Q. serrata* ($97.0 \pm 92.3$ g) > *C. henryi* ($42.0 \pm 43.4$ g).

### Crown architecture

Species richness had no effect on crown architecture, whereas species composition proved to be a significant predictor for all crown architectural variables ($P < 0.05$ for all variables). Model 2b results show that species composition had a significant effect on crown length of *C. henryi* and *Q. serrata* and on the length of the longest branch of *S. superba*. The crown length of *C. henryi* was significantly enhanced when growing with *E. decipiens* compared to both the monoculture and the combinations *C. henryi–S. superba* and *C. henryi–Q. serrata* ($P < 0.05$). Moreover,
the crown length of *C. henryi* was higher in the four-species combination compared to the monoculture (*P* < 0.05). The crown length of *Q. serrata* was significantly higher when grown with *E. decipiens* compared to the monoculture (*P* = 0.008) and the *Q. serrata–C. henryi* combination (*P* = 0.020). In addition, the crown length of *Q. serrata* was enhanced in the four-species combination compared to the *Q. serrata* monoculture (*P* = 0.028) and combination with *C. henryi* (*P* = 0.042). The length of the longest branch of *S. superba* was significantly enhanced when grown in combination with *C. henryi* compared to the monocultures, the combinations *S. superba–E. decipiens* and *S. superba–Q. serrata*, and the four-species combination (all *P* < 0.05).

**Branch demography**

Species richness had no effect on the number of branches (developed at the end of the experiment) but influenced branch turnover (*P* = 0.043) and pruning (*P* < 0.001; Fig. 3). Branch turnover was significantly enhanced in the four-species combination compared to the two-species combination (*P* = 0.047). Pruning was higher in the four-species combinations than in the two-species combinations and monocultures (*P* < 0.001). Species composition significantly affected the number of branches, branch turnover and pruning. Species identity significantly affected branch demography (all variables; Table 2).

**Discussion**

**Effects of species richness**

Our study analysed, for the first time, species richness effects on the branch demography of tree saplings. The increase in pruning and branch turnover with higher species number proved the high dynamics in the four-species combinations. Sapling individuals may adapt their crown architecture to changes in their local neighbourhood by modifying their branching arrangement (Sumida et al. 2002). These changes may be caused by the species-specific crown architecture of neighbouring saplings and differences in leaf occurrence. We interpret the observed highly dynamic branch demography as an effect of proceeding niche differentiation with regard to light harvesting in this relatively complex neighbourhood of the four-species combination.

Contrary to our expectations, we found no significant effect of species richness on the other growth and crown architectural parameters. This finding may be attributable to two factors. First, it is highly likely that diversity effects...
may evolve at a later stage of sapling development. Lang et al. (2010) analysed older tree individuals (20–100 yr) of an overlapping species pool (S. superba, Castanopsis eyrei Champ. ex Benth., Q. serrata, C. henryi) in the same study region. These authors found that crown area was affected by functional diversity. They concluded that this was due to niche separation in terms of height stratification, timing of leaf occurrence and crown density (Lang et al. 2010).

Second, species richness effects on tree growth responses (e.g. attributable to niche complementarity) might only become apparent at higher levels of diversity (Papaik & Canham 2006). The occupied niche space should increase with higher species number and thereby make niche complementarity more likely to occur.

Effects of species composition

The effects of species composition on growth, biomass allocation, crown architecture and branch demographic variables indicated that the species identity of neighbouring saplings is an important determinant of sapling growth (H2) in our experiment. This finding is in accordance with studies that demonstrate the importance of neighbourhood tree identity for growth (e.g. Massey et al. 2006; von Oheimb et al. 2011) and crown formation (Frech et al. 2003; Massey et al. 2006; Lintunen & Kaitaniemi 2010) of individual trees.

We hypothesize that several mechanisms – depending on the species involved – determine effects caused by species composition. These are evidenced by differences in the growth performance of less productive species (here: C. henryi, Q. serrata; deciduous) in the monocultures compared to combinations containing both highly productive (here: E. decipiens, S. superba; evergreen) and less productive species.

When growing together with E. decipiens, the two species Q. serrata and C. henryi grew taller and produced more biomass than when growing in monoculture or with other species. These results indicate that intra-specific competition of C. henryi and Q. serrata individuals was higher than the species inter-specific competition with E. decipiens. Massey et al. (2006) also demonstrated that height growth of saplings may increase in heterospecific plots. However, due to a higher branching of the saplings within homospecific plots, the authors did not detect any effect of species composition on above-ground biomass. In our study, the reduced competition experienced by C. henryi and Q. serrata was caused to a greater extent by the species identity of the competitor, i.e. by E. decipiens, than by the fact that it was growing with any heterospecific neighbour. Based on the observed high productivity of E. decipiens in the low-density treatment, we would have expected a reduced performance of less competitive species in combinations with E. decipiens. In addition, the biomass of E. decipiens individuals was not affected by species composition. Thus, the increased growth of C. henryi and Q. serrata in combination with E. decipiens indicate the existence of complementary or facilitative mechanisms.

Table 2. Crown architecture and branch demography. Values are means for species and density treatments. Different letters show significant differences of post-hoc Tukey tests (P < 0.05).

<table>
<thead>
<tr>
<th>Crown characteristic</th>
<th>Species means</th>
<th>Density means</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Castanea henryi</td>
<td>Elaeocarpus decipiens</td>
</tr>
<tr>
<td>Height of first branch [cm]</td>
<td>8.94</td>
<td>6.17</td>
</tr>
<tr>
<td>Crown length [cm]</td>
<td>72.89</td>
<td>106.15</td>
</tr>
<tr>
<td>Length of first branch [cm]</td>
<td>38.91&lt;sup&gt;a&lt;/sup&gt;</td>
<td>21.64&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Length of longest branch [cm]</td>
<td>52.65</td>
<td>62.14</td>
</tr>
<tr>
<td>Number of branches&lt;sup&gt;1&lt;/sup&gt;</td>
<td>6.89&lt;sup&gt;a&lt;/sup&gt;</td>
<td>21.32&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>Branch turnover&lt;sup&gt;2&lt;/sup&gt;</td>
<td>15.48&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>30.72&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>Pruning&lt;sup&gt;3&lt;/sup&gt;</td>
<td>6.23&lt;sup&gt;a&lt;/sup&gt;</td>
<td>6.85&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>1</sup> All branches exceeding 1 cm in length, counted in June 2010.
<sup>2</sup> Sum of all changes in branch number (positive and negative) from November 2009 to June 2010.
<sup>3</sup> Sum of all negative changes in branch number (November 2009 to June 2010).
The enhanced crown length of *C. henryi* and *Q. serrata* in combinations with *E. decipiens* points to complementarity of crown architecture. Complementary effects, as well as reduced inter-specific competition for light within the four-species plots compared to high intra-specific competition in monocultures, also resulted in longer crowns in both species. In contrast, *C. henryi* had shorter crowns in combination with *S. superba* than in combination with *E. decipiens*. This indicates — together with the enhanced length of the longest branch of *S. superba* in combination with *C. henryi* — negative competitive effects of *S. superba*. The effects of species composition on crown architectural variables highlight the importance of competition for light as a structuring factor of neighbourhood interactions.

**Effects of species identity**

Species identity was a strong predictor throughout the whole experiment. We found all the response variables analysed affected by species identity, which confirms our H3. Our findings also confirm the results of other studies that have described species-specific relative growth rates (Dekker et al. 2008; Suter et al. 2010) and crown architecture (Takyu 1998). Branching frequency, foliage distribution and biomass allocation to leaves significantly affect light harvesting (Niinemets 2010). Energy gain by increased light harvesting is likely to be converted to growth, and thus sapling growth and survival was related to architectural traits (Takyu 1998; Sterck et al. 2003; Dekker et al. 2008). In our study, height and diameter growth were also found to be related to the vertical and horizontal crown dimensions.

When ranking the observed species according to their productivity, the two evergreen species performed better than the two deciduous species. In contrast to our results, seedlings (<0.5 yr) of evergreen species in the same study region have been found to accumulate less biomass and show reduced phenotypic plasticity with regard to shade than deciduous species in a greenhouse experiment (Böhnke & Bruelheide unpublished data). However, the saplings in our experiment were older and thus effects of their growth performance during the seedling stage were of minor importance. The advantages of evergreen leaves, i.e. longer photosynthetic season, lower costs of replacing leaf nutrients and tougher laminae to endure frost, drought and herbivory (Givnish 2002), might also have contributed to the better performance of the evergreen species in our experiment.

Our results indicated a close relationship between species identity and branch demography. Species identity effects on branch demography were pronounced, since each of the four species had a different branch development strategy. The number of branches was low for *C. henryi* and *S. superba*. Whereas *S. superba* had the lowest degree of pruning and thus was able to invest more in stem biomass, *C. henryi* displayed high branch mortality, combined with long branches and smaller height increments. In contrast, *Q. serrata* had an intermediate number of branches and degree of pruning. High turnover rates and branch numbers of *E. decipiens* combined with large height and diameter growth suggest that this species may be able to adapt quickly to changes in the local light environment and thus optimize its foraging for light by means of a highly flexible biomass allocation to branches. The differences between species in branch demography may be seen as niche separation with regard to light harvesting. Furthermore, different branch demography results in distinct crown architecture of saplings which has important effects on ecosystem functions such as the reduction of erosive power of rain throughfall (Geißler et al. 2012).

**Effects of density**

We found a negative effect of density on diameter growth rates, but no density effects on height growth, thus partly confirming H4. Our findings are in agreement with competition studies, according to which diameter growth was often found to be influenced by the local neighbourhood (Biging & Dobbertin 1992; Canham et al. 2004; Oheimb et al. 2011). The significant reduction of biomass in all constituents of saplings of the high-density plots indicated that competition increased with increasing stand density.

In addition, density significantly affected crown architecture. A positive effect of reduced stand density on crown area was found for mature trees by Yu et al. (2003) and Hein et al. (2008). However, while the number and length of branches of loblolly pine increased with decreased density (Yu et al. 2003), this was not the case in Douglas-fir (Hein et al. 2008). Thus, effects of density on crown architecture might be species-specific and generally depend on distances to neighbours that a tree individual may encounter in the respective stand.

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Mechanisms promoting tree species coexistence


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Supporting Information

Additional supporting information may be found in the online version of this article:

**Appendix S1.** An alternative analysis of our results.

**Appendix S2.** Test of phylogenetic signal in the traits.

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