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## **Crown plasticity enables trees to optimize canopy packing in mixed-species forests**

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## Summary

1. It has been suggested that diverse forests utilize canopy space more efficiently than species-poor ones, as mixing species with complementary architectural and physiological traits allows trees to pack more densely. However, whether positive canopy packing – diversity relationships are a general feature of forests remains unclear.
2. Using crown allometric data collected for 12 939 trees from permanent forest plots across Europe, we test (i) whether diversity promotes canopy packing across forest types, and (ii) whether increased canopy packing occurs primarily through vertical stratification of tree crowns or as a result of intra-specific plasticity in crown morphology.
3. We found that canopy packing efficiency increased markedly in response to species richness across a range of forest types and species combinations. Positive canopy packing – diversity relationships were primarily driven by the fact that trees growing in mixture had sizably larger crowns (38% on average) than those in monoculture.
4. The ability of trees to plastically adapt the shape and size of their crowns in response to changes in local competitive environment is critical in allowing mixed-species forests to optimize the use of canopy space. By promoting the development of denser and more structurally complex canopies, species mixing can strongly impact nutrient cycling and storage in forest ecosystems.

**Key-words:** allometry, biodiversity and ecosystem function, canopy space filling, crown architecture, crown volume, FunDivEUROPE project, intra-specific variation, vertical stratification.

## Introduction

The vertical distribution of leaves and branches within forest canopies directly impacts light interception and understorey microclimatic conditions, making canopy structure a key determinant of productivity and nutrient cycling in forests (Prescott 2002; Purves, Lichstein & Pacala 2007; Hardiman *et al.* 2011, 2013). Recent work suggests that mixed-species forests may be able to exploit canopy space more efficiently than monocultures (Pretzsch 2014), as mixing species with complementary architectural and physiological traits enables neighbouring trees to pack their crowns more densely (Ishii & Asano 2009; Longuetaud *et al.* 2013). In fact, increased canopy packing in mixed-species stands is often invoked as a mechanism to explain positive diversity – productivity relationships in forests (Morin *et al.* 2011; Zhang, Chen & Reich 2012; Jucker *et al.* 2014a). However, much of our current understanding of how diversity influences canopy packing is based on a few well documented examples, such as the benefits of mixing European beech and Norway spruce (Pretzsch & Schütze 2005; Bayer, Seifert & Pretzsch 2013; Dieler & Pretzsch 2013; Pretzsch 2014). Determining whether optimized canopy packing is a general feature of mixed-species forests is therefore important in order to critically evaluate the effects of diversity on ecosystem functioning in forests (Nadrowski *et al.*, 2010; Scherer-Lorenzen, 2014).

Two primary mechanisms have been proposed to explain why mixed-species forests are able to make efficient use of aboveground space (Fig. 1), which we refer to here as vertical stratification and crown plasticity (Sapijanskas *et al.* 2014; Pretzsch 2014). Vertical stratification occurs when trees distribute their leaves in complementary height profiles of the canopy (Fig. 1b), and can be favoured by the coexistence of species with contrasting crown architectures (e.g., height, crown width and shape) and physiological adaptations to shade (Ishii & Asano 2009; Vieilledent *et al.* 2010; Pretzsch 2014). A classic example is the

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development of multi-layered canopies when shade-tolerant species recruit under taller, light demanding pioneers (Canham *et al.* 1994; Niinemets 2010; Morin *et al.* 2011; Hardiman *et al.* 2013). Conventional wisdom is that vertical stratification is key in allowing mixed-species canopies to maximise light interception (Hardiman *et al.* 2011; Morin *et al.* 2011; Zhang *et al.* 2012). More recently, however, it has been suggested that crown plasticity (i.e., intra-specific variation in crown morphology) may also contribute to increased canopy packing in mixed forests (Fig. 1c; Bayer *et al.* 2013; Dieler & Pretzsch 2013; Jucker *et al.* 2014a; Pretzsch 2014). Crown architecture is a highly plastic trait, and trees are known to adjust the shape and size of their crowns in response to competition with neighbours (Thorpe *et al.* 2010; Vieilledent *et al.* 2010; Seidel *et al.* 2011a). For instance, under crowded conditions trees tend to invest heavily in height growth and less in crown development (Henry & Aarssen 1999; Muth & Bazzaz 2003; Lines *et al.* 2012). Under the assumption that trees in mixture compete less fiercely for light than those in monoculture (e.g., because species access different strata of the canopy and exhibit varying degrees of shade tolerance), species mixing can therefore promote canopy packing by enabling trees to expand their crowns (Pretzsch & Dieler 2012; Jucker *et al.* 2014a).

Here we take advantage of a novel research platform designed specifically to investigate how diversity influences ecosystem function in forests to comprehensively test the effects of species mixing on canopy packing across Europe. Using crown allometric data collected for 12 939 trees we test whether species mixing promotes canopy packing across major European forest types (**H1**), and determine whether positive canopy packing – diversity relationships are the result of vertical stratification (**H2**) and/or changes in the crown allometries of individual trees (**H3**).

## Materials and methods

### STUDY DESIGN

The study was conducted in the FunDivEUROPE permanent forest plot network ([www.fundiveurope.eu](http://www.fundiveurope.eu)), which was established in 2011 for the specific purpose of testing the effects of biodiversity on ecosystem functioning in mature European forests. A detailed description of the FunDivEUROPE network is available in Baeten *et al.* (2013). Briefly, the plot network consists of 209 permanent forest plots, 30 x 30 m in size, distributed among six sites across Europe. Field sites represent major European forest types, and include boreal forests in Finland, hemiboreal and mixed broadleaved-coniferous forests in Poland, beech forests in Germany, mountainous beech forests in Romania, thermophilous deciduous forests in Italy and Mediterranean mixed forests in Spain. At each site, plots contain different combinations of locally dominant tree species, and range in species richness from 1-3 in Finland, 1-4 in Romania, Germany and Spain, and 1-5 in Italy and Poland. The species pool includes conifers, deciduous broadleaves and evergreen broadleaves, with each target species represented in all species richness levels. To allow meaningful comparisons among species richness levels, plots were selected on the basis of three main criteria: (i) species in mixture had to have similar relative abundances (i.e., high evenness); (ii) plots were established exclusively in mature forests stands which have received minimal management intervention in recent years; (iii) plots within a site had to share similar environmental conditions (e.g., elevation, topography and soil quality).

### ALLOMETRIC DATA AND CROWN VOLUME ESTIMATION

Across all plots, stems  $\geq 7.5$  cm in diameter were identified to species and permanently marked (12 939 stems in total). For each stem we recorded diameter at breast height (*DBH*), and used a vertex hypsometer (Haglöf AB, Sweden) to measure tree height (*H*), maximum

crown radius ( $CR_{max}$ ; as the average of two orthogonal measurements) and crown depth ( $CD$ ).

These field data were used to estimate the crown volume ( $CV$ ; in  $m^3$ ) of individual trees. In

the simplest case, crowns can be approximated by a cylinder. However, this inevitably overestimates  $CV$ , as it assumes no tapering in crown radius nearing the top of the tree.

Critically, it also fails to account for differences in crown shape among species or functional groups (Purves *et al.* 2007). We therefore chose to model crown volume as a parabolic cone,

with an additional shape parameter ( $\beta$ ) which allows the curvature of the crown to vary among conifer and broadleaf species (see Appendix S1 in Supporting Information).  $CV$  is

estimated by integrating the function which describes how crown radius changes with tree height (Caspersen *et al.* 2011):

$$CV = \int_{H-CD}^H \pi (f(h))^2 dh \quad (1)$$

where  $f(h)$  is the crown radius at a given height  $h$  from the base of the crown ( $CR_h$ ). We chose the following functional form to represent how crown radius varies from the base to the top of the crown:

$$CR_h = CR_{max} \left( \frac{CD-h}{CD} \right)^\beta \quad (2)$$

where  $\beta$  determines the shape of the crown, ranging from cylindrical when  $\beta$  approaches 0 to cone-shaped when  $\beta = 1$ . Substituting  $f(h)$  with equation (2) allows a general formula for estimating  $CV$  to be derived (see Appendix S1 for step-by-step integration):

$$CV = \frac{\pi CR_{max}^2 CD}{2\beta + 1} \quad (3)$$

Average  $\beta$  values for conifer and broadleaf species were obtained from the literature (Purves *et al.* 2007), allowing us to account for differences in crown shape of the two main tree functional groups present in our study. Ideally, estimates of  $CV$  based on equation (3) would also incorporate both inter- and intra-specific variation in  $\beta$ . However, this proved impractical as it would have required obtaining multiple crown radius measurements at successive height intervals for nearly 13000 trees. Nonetheless, we expect equation (3) to provide a robust approximation of  $CV$ , as most of the inter-tree variation in  $CV$  is driven by the numerator of the equation (see Appendix S1), all components of which were measured at the individual tree level.

#### OBSERVED AND PREDICTED CANOPY PACKING

We define canopy packing as the proportion of aboveground space potentially available to trees which is actually occupied by crowns (Fig. 1):

$$\text{Canopy packing} = \frac{\Sigma CV}{\text{Plot area} \times [H_{maxj} - (H - CD)_{minj}]} \quad (4)$$

where  $\Sigma CV$  is the sum of the crown volumes of all standing trees within a plot, and is equivalent to total canopy volume; plot area is 900 m<sup>2</sup> for all plots; and  $H_{maxj}$  and  $(H - CD)_{minj}$  are, respectively, the maximum tree height and the height of the lowest live branch recorded in site  $j$  (i.e., invariant among plots within a site). The numerator of equation (4) corresponds to the space actually occupied by tree crowns, while the denominator defines the space in which trees could potentially grow and is the same for all plots within a site. Canopy packing values range between 0 (no canopy) and 1 (fully occupied space). Although canopy packing (as defined above) is inherently related to the cumulative leaf area of trees within a plot, the two measures will not necessarily covary perfectly as leaf density can vary strongly within crowns (e.g., Seidel *et al.* 2011b). Nevertheless, crown volumes are expected to

provide an adequate representation of the forest canopy and have the advantage of relating directly to how trees partition aboveground space.

For each plot, we used equation (4) to calculate two alternative measures of canopy packing based on different estimates of  $CV$  for individual trees. We refer to these as observed and predicted canopy packing, and use them to tease apart the effects of vertical stratification and crown plasticity on canopy space filling. Observed canopy packing is estimated directly from field data (i.e.,  $CR_{max}$  and  $CD$  values measured in the field are used to calculate each tree's  $CV$ ), and therefore incorporates both the effects of vertical stratification and crown plasticity. For predicted canopy packing, each tree's crown dimensions are estimated from an allometric model designed to remove the effects of crown plasticity (Appendix S2). Specifically, we fitted regression models of  $\log(CV)$  vs  $\log(DBH)$  for each species and used these models to predict the  $CV$  of each tree based exclusively on its size. By removing intra-specific variation in  $CV$  other than that associated with tree size, predicted canopy packing values account only for the effects of vertical stratification. Regressions were fitted using ordinary least squares regression (as opposed to standardised major axis regression), as the models needed to generate predictions of  $CV$  for each tree (Warton *et al.* 2006). Because models were fitted on a logarithmic scale, when predictions were back-transformed to arithmetic scale a correction factor was applied to account for log-normally distributed errors (Baskerville 1972). This consisted of multiplying predicted values by  $e^{(MSE/2)}$ , where MSE is the mean square error of the regression, and is a necessary step to avoid systematic underprediction (Mascaro *et al.* 2011).

#### HYPOTHESIS TESTING

We used mixed-effects modelling to test hypothesized relationships between species mixing and canopy packing in forest. All analyses were implemented in R (3.0.1; R Development



Core Team 2013), with package *lme4* being used to fit mixed-effect models. For the purposes of this study, 10 plots were excluded from the analysis due to the presence of non-target species within the stand, as insufficient allometric data were available to robustly model *CV* for these species (Appendix S3).

### *H1: Canopy packing – diversity relationships*

To test whether canopy packing increases with diversity (**H1**), we used mixed-effects linear regression to model observed canopy packing as a function of species richness, plot basal area and site. We included basal area as a covariate in the model to account for its direct influence on total canopy volume, while site was modelled as a random effect to control for differences in mean canopy packing among forest types (see Appendix S3 for comparison with alternative model structures). Canopy packing was logit-transformed prior to model fitting to account for its values being bounded between 0 and 1. Because species richness and plot basal area are weakly correlated with one another (Pearson's correlation coefficient = 0.13; Fig. S7), collinearity is not expected to affect parameter estimates in the model (Dormann *et al.* 2013).

### *H2: Vertical stratification*

If greater canopy packing is the result of increased vertical stratification (**H2**), then a positive relationship between canopy packing and species richness should be observed in the absence of crown plasticity. To test this, we modelled predicted canopy packing (which excludes intra-specific variation in crown dimensions) as a function of species richness, again accounting for basal area and site effects in the mixed model.

### *H3: Crown plasticity*

The alternative hypothesis is that increased canopy packing in mixed-species forests depends critically on the ability of individual trees to expand their crowns when growing in mixture

(H3). If this were the case, we would expect species richness effects to be underestimated when modelling predicted canopy packing values, as these purposely exclude the role of crown plasticity. To test this, we quantified the difference between observed and predicted canopy packing for each plot, and then used mixed-effects models to determine whether this difference increases with species richness.

To complement this, we also performed a species-level analysis to determine whether trees growing in mixture have larger crowns than those in monoculture. This was done by extending the regression models of  $\log(CV)$  vs  $\log(DBH)$  – which we used to generate predicted canopy packing values – to include a species richness term. Plot basal area was also included as a covariate in the models to account for the effects of crowding on  $CV$  (Lines *et al.* 2012). To determine whether changes in  $CV$  result from vertical or horizontal crown expansion, we used this same approach to separately model the effects of diversity on  $CR_{max}$ ,  $CD$  and  $H$ . To avoid misinterpreting the effects of species mixing on crown plasticity, only species for which monoculture treatments were replicated at least twice were included for these analyses ( $n = 19$ ).

## Results

### H1: CANOPY PACKING – DIVERSITY RELATIONSHIPS

Across the plot network observed canopy packing increased significantly with species richness (Table 1; Fig. 2a). Across sites, canopy packing was lowest in Spain and peaked in central European temperate forests (Germany and Poland; inset in Fig. 2a). Yet despite mean canopy packing values varying considerably among sites, the positive effect of diversity on observed canopy packing was similar across forest types ( $\Delta AIC = 6$  when comparing models with and without a random slope term allowing species richness effects to vary among sites;

Table S2 and Fig. S6). Plots with a higher basal area also exhibited greater observed canopy packing (slope =  $0.028 \pm 0.020$ ;  $P = 0.038$ ). This effect was largely independent from that of species richness, as mixed-species plots do not differ in basal area from monocultures (Fig. S7).

## H2: VERTICAL STRATIFICATION

Predicted canopy packing values, which assume that a tree's *CV* is non-plastic and determined solely by its size, also showed a positive association with species richness (Fig. 2a). However, the effect of diversity was decidedly weaker than in the case of canopy packing values obtained from field measurements, and the inclusion of the species richness term in the model received only marginal support (Table 1). Instead, predicted canopy packing values were primarily determined by the basal area of the plot (slope =  $0.038 \pm 0.018$ ;  $P = 0.007$ ).

## H3: CROWN PLASTICITY

The difference between observed and predicted canopy packing varied strongly in relation to species richness, with mixed-species plots exhibiting a significantly greater difference between the two measures (Table 1; Fig. 2b). Differences between observed and predicted canopy packing values did not vary systematically among sites (inset in Fig. 2b), suggesting that changes in crown allometry of individual trees play a critical role in promoting canopy packing across forest types.

The importance of crown plasticity as a driver of canopy packing was further highlighted by species-level analyses, which revealed strong intra-specific variability in *CV* related to both species mixing and crowding (Fig. 3). For a given stem diameter, trees in mixture generally had larger crowns than those in monoculture (across-species slope of  $\log(CV)$  vs species richness =  $0.081 \pm 0.014$ ). Specifically, seven out of 19 species showed a significant increase

in *CV* when growing in mixture, with only one species exhibiting the opposite trend (Fig. 3a). Increased *CV* resulted from both lateral and vertical crown expansion of trees in mixture (Fig. 4; Appendix S4), and the effect persisted even after accounting for the negative effect of crowding (i.e., total basal area of the plot) on the crown size of individual trees (Fig. 3b; across-species slope of  $\log(CV)$  vs basal area =  $-0.011 \pm 0.002$ ). This suggests that for a given crowding density, trees in mixture develop larger crowns than those in monoculture. Given that species richness and basal area are weakly correlated with one another in our plot network (Fig. S7), the effect of crowding on *CV* occurred independently from that of species richness.

## Discussion

We found that canopy packing increased with diversity across forests in Europe (Fig. 2), indicating that mixed-species forests are able to make more efficient use of aboveground space compared to monocultures (Morin *et al.* 2011; Pretzsch 2014). Despite major differences in species composition and climate among study sites, the effect of species richness on canopy packing was strongly conserved across forest types (Fig. S6). Both vertical stratification and crown plasticity were important in allowing mixtures to optimize canopy space filling. However, of the two processes crown plasticity emerged as the stronger driver of canopy packing (Fig. 2), as most tree species were found to expand their crowns when growing in mixture (Figs 3 and 4). Here we review our results in light of the current literature before discussing the implications of our findings for biodiversity – ecosystem function research in the context of forests.

## CROWN PLASTICITY

The ability of trees to adjust the shape and size of their crowns in response to changes in their local competitive environment emerged as a critical element promoting efficient canopy packing in mixed forests (Vieilledent *et al.* 2010; Pretzsch & Dieler 2012). On average, trees growing in mixture developed longer lateral branches and deeper crowns (Fig. 4), resulting in a 38% increase in *CV* (Fig. 3). A number of recent studies have reported similar patterns for select combinations of species, such as mixtures of European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) in central European forests (Pretzsch & Schütze 2005; Bayer *et al.* 2013; Dieler & Pretzsch 2013; Pretzsch 2014). This work has shown that complementary crown morphologies, branching patterns and abilities to tolerate shade of beech and spruce trees allow both species to develop larger crowns when mixed together (Bayer *et al.* 2013). Our results suggest that increased *CV* of individual trees growing in mixture is a general feature of diverse forests (Sapijanskas *et al.* 2014; Jucker *et al.* 2014a).

The fact that trees in mixture develop larger crowns is strongly indicative of the fact that niche partitioning processes – likely driven by complementary crown architectures and contrasting physiological adaptations of leaves to shade (Appendix S5) – lessen the intensity of competition for light in mixed forests (Ishii & Asano 2009; Thorpe *et al.* 2010; Vieilledent *et al.* 2010; Seidel *et al.* 2011a; Longuetaud *et al.* 2013). Trees which are subjected to strong competition for light tend to develop thin, shallow crowns, and invest heavily in height growth (Henry & Aarssen 1999; Muth & Bazzaz 2003; Lines *et al.* 2012). This occurs as trees extend their branches vertically to intercept overhead light and is reinforced by mechanical abrasion between neighbouring stems, a process which manifests itself in the form of crown shyness (Pretzsch 2014). As competition for light lessens, trees allocate a greater portion of fixed carbon towards the development of lateral branches and less towards vertical growth (Vieilledent *et al.* 2010; Seidel *et al.* 2011a; Forrester & Albrecht 2014). This

is precisely what we observe when comparing trees growing in monoculture *versus* mixture. The average tree in mixture was 1.6 m shorter than its counterpart in monoculture, and instead exhibited considerably longer and lower-lying horizontal branches (Fig. 4). The fact that trees are able to plastically adjust the shape and size of their crowns is critical in allowing them to capitalize on reduced competition in mixed forests, and ultimately means that trees in mixture can pack more densely without exhibiting strong reductions in crown size (Fig. 3).

#### VERTICAL STRATIFICATION

Compared to crown plasticity, vertical stratification emerged as a rather weak driver of canopy packing across our plot network (Table 1; Fig. 2a). This differs somewhat to the results of previous studies which have shown that mixing species which distribute their leaves in complementary height profiles of the canopy is critical in allowing trees to pack more densely (Hardiman *et al.* 2011; Vilà *et al.* 2013; Sapijanskas *et al.* 2014; Pretzsch 2014). One explanation for the limited importance of vertical stratification in promoting canopy space-filling we find in our study is that developing vertically structured canopies requires mixing species with strongly contrasting crown allometries. For instance, recent work in Mediterranean forests showed that mixing tall, light-demanding pine trees with shorter, shade tolerant oaks increased vertical stratification in the canopy, resulting in greater productivity at the stand level (Jucker *et al.* 2014a). However, because the FunDivEUROPE plot network focuses primarily on canopy dominant trees and includes only a limited number of understorey tree species (e.g., *Ostrya carpinifolia* in Italy, *Carpinus betulus* in Poland and *Quercus* species in Spain), opportunities for achieving vertical stratification may be limited compared to forests that are more functionally diverse (e.g., Sapijanskas *et al.* 2014). Consistent with this interpretation is the fact that we found little evidence of species richness promoting stand basal area in our plot network (Fig. S7), something which has instead

emerged clearly from previous work using European forest inventory data which cover a wider range of tree species and functional groups (Vilà *et al.* 2013).

Although vertical stratification was a comparatively weaker driver of positive canopy packing – diversity relationships than crown plasticity, evidence that species mixing promotes greater vertical structuring of the canopy can be seen in both plot- and species-level data (Table 1 and Fig. 2a; Table S4). Far from being unimportant, these differences in crown allometry among species are critical in allowing individual trees to plastically adapt the size and shape of their crowns (Pretzsch & Dieler 2012; Jucker *et al.* 2014a). Our results show that species mixing can promote canopy packing even in the absence of strong vertical stratification, largely as a result of crown plasticity. However, for this to be the case coexisting species need to exhibit at least some degree of niche partitioning, either in terms of crown dimensions, leaf vertical profiles or abilities to tolerate shade. In this respect, vertical stratification and crown plasticity can be thought of as complementary mechanisms, the relative importance of which is likely to depend on the functional composition of forests.

#### IMPLICATIONS FOR BIODIVERSITY – ECOSYSTEM FUNCTION RESEARCH IN FORESTS

Growing evidence suggests that diverse forests ecosystems are able to function more efficiently and deliver a higher standard of ecosystem services than species poor ones (Nadrowski *et al.*, 2010; Scherer-Lorenzen, 2014). For instance, mixed-species forests have been shown to be more productive (Zhang *et al.* 2012; Vilà *et al.* 2013; Jucker *et al.* 2014b) and cycle nutrients more readily (Scherer-Lorenzen, Luis Bonilla & Potvin 2007; Schwarz *et al.* 2014), while concurrently providing habitat for a greater number of associated species (Castagneyrol & Jactel 2012). However, the processes which underlie positive biodiversity – ecosystem function relationships in forests remain poorly understood. The fact that species mixing increases canopy packing provides a mechanism for explaining several of these

patterns (Fig. 5). By promoting the formation of denser and more structurally complex canopies, species mixing can maximise light interception at the stand level (Binkley *et al.* 2013), thereby increasing forest productivity (Hardiman *et al.* 2011, 2013; Morin *et al.* 2011; Reich 2012; Coomes *et al.* 2014). Canopy density also influences microclimatic conditions in the understorey, attenuating fluctuations in temperature and increasing soil moisture (von Arx *et al.* 2013; Crockatt & Bebbber 2014). Coupled with likely increases in leaf litter production (Jonckheere *et al.* 2004; Scherer-Lorenzen *et al.* 2007), the greater ability of dense canopies to retain moisture helps explain faster decomposition and nutrient cycling rates in mixed forests (Ryan, Binkley & Fownes 1997; Janssens *et al.* 2001; Prescott 2002; Schwarz *et al.* 2014; Crockatt & Bebbber 2014). As an added benefit, structurally complex canopies favour the coexistence of greater numbers of species (e.g., birds, bats, insects, understorey plants; Tews *et al.* 2004; Barbier, Gosselin & Balandier 2008; Simonson, Allen & Coomes 2014), while the cooling effect of a dense overstorey can mitigate the impacts of macroclimate warming (De Frenne *et al.* 2013). Managing forests with the objective of increasing canopy density and structural complexity holds promise for enhancing the carbon sequestration and storage potential of forest ecosystems, as well as safeguarding their biodiversity. Our study suggests that maintaining tree species diversity offers a simple solution towards achieving these management goals.

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### Data accessibility

Canopy packing data are available from the FunDivEUROPE online data portal, accessed through URL: <http://fundiv.befdata.biow.uni-leipzig.de/datasets/412> (Jucker *et al*, 2015)

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### **Supporting information**

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

**Appendix S1:** Estimating crown volume of individual trees.

**Appendix S2:** Canopy packing models.

**Appendix S3:** Predicted canopy packing.

**Appendix S4:** Crown expansion and light interception.

**Appendix S5:** The influence of shade tolerance on canopy packing.

## Tables

**Table 1:** Outputs of linear mixed-effect models testing hypothesized relationships between canopy packing and species richness. Slopes ( $\pm$  95% confidence intervals) and  $P$ -values (based on Satterthwaite approximation, as implemented in the *lmerTest* package) are reported for the species richness term in each model.  $\Delta$ AIC scores refer to comparisons between models with and without a species richness term. Conditional  $R^2$  values correspond to the proportion of variance explained by both fixed and random effects (Nakagawa & Schielzeth 2013).

Canopy packing model	Hypothesis	Slope (CI <sub>95</sub> )	$P$ -value	$\Delta$ AIC	$R^2$
Observed	H1	0.125 (0.072)	<0.001	-9.2	0.80
Predicted	H2	0.049 (0.054)	0.076	-1.2	0.88
Obs. – Pred.	H3	0.016 (0.009)	<0.001	-9.1	0.13

## Figure legends

**Fig. 1:** Conceptual diagram of species richness effects on canopy packing. Panel (a) provides a 3D illustration of canopy packing as defined in equation (4). The sum of the individual tree crown volumes gives the canopy volume of the plot, while the shaded region in grey corresponds to the aboveground space potentially available for trees to grow in. This space is invariant among plots within a site, and is delimited (i) horizontally by the size of the plot (30 x 30 m) and (ii) vertically by the distance between the maximum tree height ( $H_{\max}$ ) and the lowest crown base  $[(H - CD)_{\min}]$  measured at a given site. Mixed-species forests can optimize canopy packing through (b) vertical stratification and/or (c) crown plasticity. Mixing species which occupy complementary strata of the canopy can promote canopy packing by increasing vertical stratification. Alternatively, decreased competition in mixed stands can allow individual trees to expand their crowns.

**Fig. 2:** Effect of species richness on (a) observed (accounting for both crown plasticity and vertical stratification effects; black line) and predicted canopy packing (vertical stratification effect only; red line), and (b) difference between observed and predicted ( $\Delta$ ) canopy packing (crown plasticity effect; blue line). Lines correspond to fitted relationships of mixed-effects linear models, with shaded regions showing the 95% confidence interval range (based on 1000 bootstrap replicates). Inset boxplot in panel (a) shows the range of observed canopy packing values at each study site, while inset boxplot in panel (b) show the distribution of  $\Delta$  canopy packing values per site.

**Fig. 3:** Change in canopy volume ( $CV$ ) as a function of (a) species richness and (b) plot basal area. Circles correspond to slopes ( $\pm$  95% confidence intervals) of multiple-regression models relating  $\log(CV)$  to tree size ( $DBH$ ), species richness and plot basal area. Filled circles indicate slopes significantly different from zero ( $P < 0.05$ ). Solid vertical lines show the across-species effects, with shaded 95% confidence intervals. Species names are abbreviated using the first three letters of the genus and species name, with the country of origin reported in brackets.

**Fig. 4:** Average crown profile of a tree growing in monoculture (left) and species mixture (right). Across-species parameter estimates were used to predict  $CR_{max}$ ,  $CD$  and  $H$  for a tree of mean size ( $DBH = 21$  cm) in monoculture and mixture (see Table S3 for parameter values). Predictions are based on average plot basal area values ( $30.8 \text{ m}^2 \text{ ha}^{-1}$ ) and crown profiles were drawn assuming  $\beta = 0.33$  (average shape parameter across conifer and broadleaved species). Shaded regions indicate 95% confidence intervals of crown dimensions (based on 1000 bootstrap replicates).

**Fig. 5:** Schematic diagram illustrating how increased canopy packing in mixed-species forests can promote positive biodiversity – ecosystem function relationships in forest



ecosystems. Primary mechanisms are represented by bold arrows, while secondary pathways are marked by dashed arrows in grey. Key references for each process are marked in grey.







