Terrestrial laser scanning reveals differences in crown structure of *Fagus sylvatica* in mixed *vs.* pure European forests

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ABSTRACT

Competition with neighboring trees of different species can affect crown size and shape. However, whether intra-specific differences in crown characteristics in mixed stands compared to pure stands are dependent on site conditions remains poorly understood. We used terrestrial laser scanning (TLS) to examine the differences in *Fagus sylvatica* crown characteristics at four sites, each of which contained pure stands of *F. sylvatica* and their mixture with *Pinus sylvestris*. These sites covered the area where the mixture occurs in Europe from south to north, representing a gradient of *F. sylvatica* productivity, defined as the mean increment of annual volume growth in pure *F. sylvatica* stands. Despite the large range in productivity, *F. sylvatica* trees in mixtures had larger crowns regardless of site conditions, with a higher proportion of their crown volume in the lower canopy compared to trees in pure stands. Larger crown volumes were related to higher live crown ratios and greater crown expansion, depending on the site. The magnitude of the mixing effect was variable among the crown characteristics evaluated, but overall our findings provide evidence that for a given species combination and density, the effect of mixture increased in the two most productive sites. TLS-derived novel crown metrics revealed that the mixing effect was affected by productivity, which was not captured by traditionally measured crown variables.

1. Introduction

Crown morphological characteristics, such as crown size and crown shape or profile (Power et al., 2012), are central to many aspects of forest functioning and productivity. Tree species and tree size have been found to be the primary drivers of most crown shape variables. However, crown characteristics can vary with age and canopy position (Ishii et al., 2013), with stand density resulting from natural mortality or thinning (Garber and Maguire, 2005; Weiskittel et al., 2009), and with stand structure for a given species composition (Forrester et al., 2016; Río et al., 2015). Although crown characteristics are partially controlled by genotype, individuals are highly plastic in adjusting their crown morphology to their local biotic or abiotic environment (Barbeito et al., 2014; Li et al., 2014). As a result, the type and

arrangement of neighboring competitors are major factors affecting crown development (Kaitaniemi and Lintunen, 2010; Vieilledent et al., 2010). Mixing species with complementary crown morphologies can modify the quantitative relations between the dimensions of various tree compartments (stem, branches, foliage), known as tree allometry (Pretzsch, 2014; Guisasola et al., 2015). Such changes can result in an increase in the variability of individual crown size and shape for a given species in mixed stands. This can influence stand occupancy and increase forest light interception and growth by individual crowns (Forrester and Albrecht, 2014; Sapijanskas et al., 2014) Therefore, understanding the effect of mixture on modifying canopy heterogeneity can provide insights into the resource-use efficiency and functioning of mixed forests compared to pure stands.

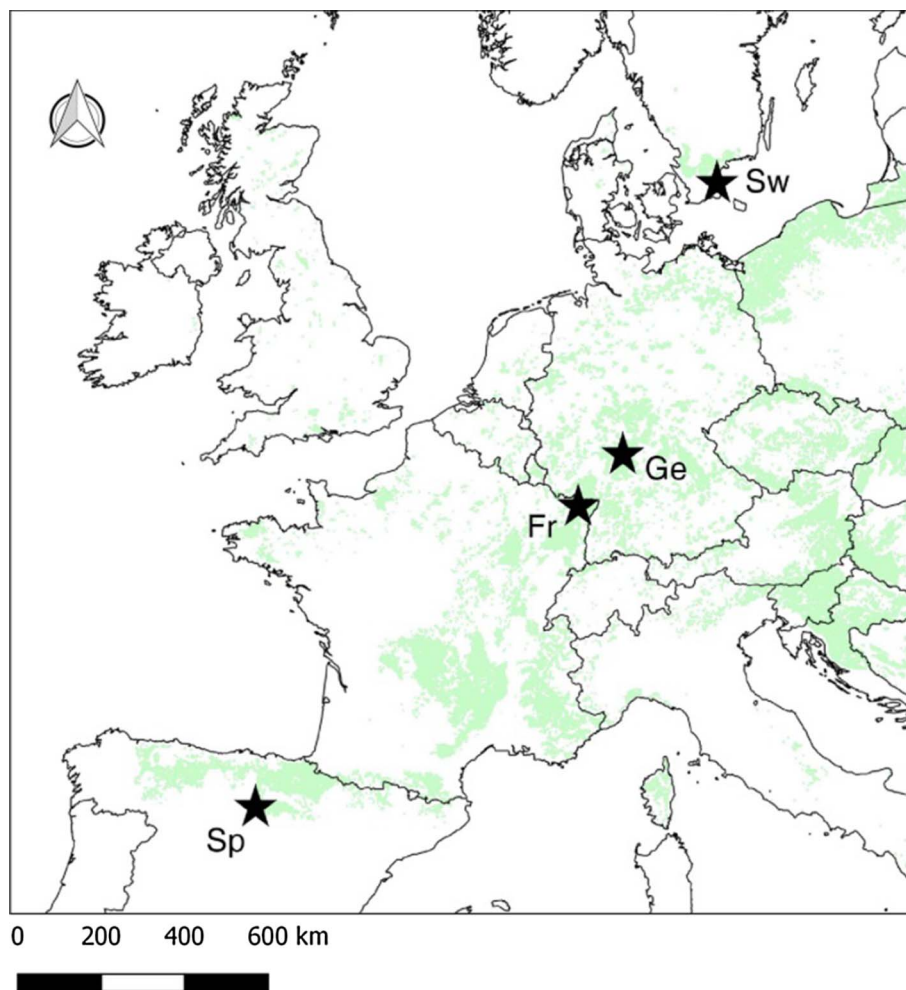However, the complementary effects caused by mixture can change

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Fig. 1. Study locations of the four *F. sylvatica* pure stands and mixed stands with *P. sylvestris* (Spain-Sp; France-Fr; Germany-Ge; Sweden-Sw). In green, the distribution area where *F. sylvatica* – *P. sylvestris* mixed stands occur in Europe based on the EFI Tree Species Maps for European Forests (Brus et al., 2011).

with resource availability. Crown structural differences between mixed and pure stands are likely to vary with nutrient and water availability (Pretzsch et al., 2016). Soil fertility may alter competitive interactions in multispecies forests impacting growth and branch number and size (Coates et al., 2013; Weiskittel et al., 2007). When water deficits occur, larger crowns could be disadvantageous because even if they absorb more light (Forrester and Albrecht, 2014), they also have larger transpirational surfaces, which may limit the intra-specific variability (Valladares et al., 2007).

Quantifying crown characteristics in mature stands has been difficult in the past as field-based methods are labor-intensive and imprecise (Bayer et al., 2013). To overcome this obstacle, high-resolution Terrestrial Laser Scanning (TLS) has emerged as an alternative non-destructive tool to obtain crown measurements (Calders et al., 2015; Dassot et al., 2011). TLS provides three-dimensional (3D) descriptions of trees, and thus enables more accurate crown metrics than those traditionally used (Seidel et al., 2015). TLS has recently been used for describing crown displacement (Seidel et al., 2011), crown profiles (Ferrarese et al., 2015), crown volume and surface area (Fernández-Sarría et al., 2013; Metz et al., 2013), branch angles (Bayer et al., 2013) or leaf area and leaf orientation (Bailey and Mahaffee, 2017; Béland et al., 2011; Delagrange and Rochon, 2011). These descriptors may be used to analyze crown competition (Metz et al., 2013) and patterns in canopy space exploration (Seidel et al., 2013). The use of these variables may contribute towards more accurately quantifying the way individual tree crowns of a given species are influenced by neighboring competitors of the same or different species in spatially diverse canopies such as those found in mixed stands. For instance, recent studies

have found differences in the crown volume derived by TLS of pure and mixed stands (Bayer et al., 2013; Martin-Ducup et al., 2016). However, the use of comprehensive data on crown morphology from TLS-based measurements is still at an early stage (Seidel et al., 2015), with most TLS studies dealing with crown morphology focusing on the detailed characterization of limited sample sizes at single locations. Consequently, previous TLS studies have not been able to determine whether differences in crown morphology in mixed forests *versus* pure forests are constant or vary along large latitudinal gradients.

In this study, we used TLS to collect detailed 3D-crown morphology data for one of the most widely distributed species mixtures in Europe (late-successional *Fagus sylvatica* and pioneer *Pinus sylvestris*) at forests with different site productivity and growth-limiting factors across Europe. We aimed to quantify how mixing influences crown morphology of individual trees. Our objectives were: (1) to test the effect of mixture on crown size and shape; we hypothesized that differences are more apparent at productive sites, where crown growth is not limited by factors other than competition for light; (2) to test the variability in crown allometry between pure and mixed stands; we hypothesized that variability is higher in mixtures because the local canopy neighborhood is more heterogeneous; and (3) to evaluate if novel TLS-derived variables reveal effects of mixing on crown morphology not detected with the metrics traditionally used in the field to describe tree crowns. These questions were addressed on *F. sylvatica*, which forms most mixed stands in Central Europe, and has a demonstrated capacity to effectively occupy canopy space as a result of its high crown plasticity (Pretzsch, 2014; Schröter et al., 2012).

2. Material and methods

2.1. Experimental sites

Crown characteristics were examined in four sites representing a gradient of *F. sylvatica* productivity (i.e. quantified as the mean increment of annual volume growth in the period 2009–2013 for pure stands of *F. sylvatica*; Table S1) within the network installed by members of the COST action EuMixFor (Heym et al., 2017). The four sites cover the range of distribution of the mixed *F. sylvatica-P. sylvestris* forests, from its southernmost range in Spain to its northern limit in Sweden, including two sites in Central Europe: France and Germany (Fig. 1).

As our stands vary widely in latitude and altitude, the CVP index (Paterson, 1956) was used to characterize growth conditions, where $CVP = T_v/T_a \times P \times G/12 \times E/100$ is based on the T_v (mean temperature of the warmest month, in °C), T_a (difference of the mean temperature of the warmest month minus mean temperature of the coldest month, in °C), P (mean annual precipitation, in *mm*), G (number of months out of twelve with mean temperature ≥ 3 °C), and $E\%$ (evapotranspiration intensity, as a function of geographical latitude, in degrees). Each site contains two fully stocked study stands, not thinned during the last decade with most trees in full crown contact (Fig. 2).

All sites present similar age and soil conditions (Table S1) with a pure *F. sylvatica* stand and an intimate mixture with *P. sylvestris* (i.e. trees mixed on a tree-by-tree basis as opposed to patches of individuals of each species mixed with patches of the other species). Twenty *F. sylvatica* trees belonging to the upper canopy layer (dominant or co-dominant trees; Table 1) were selected per plot in pure and mixed stands in the four sites as trees of interest representing a total of 160 trees.

2.2. Laser scanning and plot digitisation

Terrestrial laser scanners make possible the non-contact three-dimensional (3D) digitisation of objects or physical scenes. The digitisation relies on a thin laser beam which is deflected in millions of directions (defined by azimuth and angle to the vertical) to scan the scene. For each direction, the laser beam is reflected by the first encountered target. The fraction of light that returns to the scanner allows a distance to be computed and, therefore, a 3D point to be recorded at the location where the laser was intercepted. Millions of points are recorded over the surface of the objects to create a 3D point cloud. Since a scanner only digitalises the visible side of the objects, several scans have to be performed on different sides of the objects to allow for their complete digitalisation. Finally, the 3D representation of the scene requires 3D modelling steps to provide the metrics of the objects (Dassot et al., 2011).

The plots were digitised between December 2014 and March 2015, i.e. during the leafless season of *F. sylvatica*. Each plot was digitised with a phase-based FARO Focus³ᴰ 120 scanner with settings providing sufficient point cloud density at the top of the trees in reduced scanning

times (Table S2). Scanning resolution was chosen to theoretically allow for overlapping between two successive laser footprints (based on the beam divergence and the distance between two successive footprints at a given distance provided by the manufacturer) ensuring the complete coverage of the space. These settings allowed for the digitisation of the woody structure of the trees to the thinnest axes. Several scans were performed within the plot; we chose to scan the area with a regular grid of 6–7 m grid spacing (as sometimes scan positions may be occupied by trees or blocked by branches) in order to cover the forest scene and obtain a description of all of the tree crowns that would allow us to identify branch tips and thus to accurately define crown size and shape (Wilkes et al., 2017). FARO Scene 4.8 software was then used to merge the multiple point clouds into one co-registered point cloud, based on 15–35 high-reflectance reference spheres with a diameter of 14 or 14.5 cm, homogeneously placed within plots prior to scanning such that at least four spheres were visible from each scan position. This scanning protocol made it possible to obtain an accurate 3D representation of each plot and of their individual trees (Fig. 3a). TLS data analysis then consisted of (i) extracting each selected tree from the global point cloud of the plot, and (ii) deriving dendrometric variables for each extracted single tree.

2.3. Single tree segmentation

The aim of the segmentation steps was to extract an individual point cloud for each target tree from the global point cloud of the plot. Each tree of interest was marked with a tape in the field to facilitate their detection in the global point cloud of the plot in FARO Scene software. In order to reduce computing times, a subplot centred on the tree of interest was selected and saved from FARO Scene as a .xyz file (Fig. 3b). The subplot was then imported in the CompuTree software, which is dedicated to processing laser scanning data of forest scenes (CompuTree 2010). Data points were resampled at 1pt/0.5 cm (from 1 pt/6 mm; Table S2) to further reduce computing times and to homogenise cloud density (i.e. reduce the oversampled data around the stems and ground close to the scanner). The tree of interest was then individually segmented from the subplot using a k-nearest neighbor algorithm (Fig. 3c and d). The tree was then visually inspected in the metrology software PolyWorks (InnovMetric Software Inc.) to manually remove, if needed, remaining data points unrelated to the tree.

2.4. Crown characteristics assessment

Virtual dendrometric measurements were performed on each single tree point cloud to derive diameter at breast height (DBH, 1.3 m above the ground), total tree height (TTH), crown length (CL), and crown volume (CV). DBH was assessed using PolyWorks by selecting the points in a 2-cm-thick slice at a height of 1.30 m above the ground and fitting a circle through it (least-squares fitting). TTH and CV were assessed using CompuTree. TTH was assessed as the vertical distance between the highest and the lowest point of the tree point cloud. CV

Fig. 2. Photographs of pure *F. sylvatica* stand canopy (left) and the mixed *F. sylvatica* – *P. sylvestris* stand canopy (right) in Spain with stand densities of 2910 trees ha⁻¹ and 2868 trees ha⁻¹ respectively.

Table 1
Mean value, standard deviation and range of DBH (diameter and breast height), CL (crown length rescaled; 0–1) for the maximum CW (crown width rescaled; CW/CL), LCR (live crown ratio) and SCI (space capture index) for *F. sylvatica* trees in the pure (P) and mixed stands (M) in France (Fr), Spain (Sp), Sweden (Sw) and Germany (Ge); *n* = 20 trees per site and stand type.

| Site		DBH (cm)			CV (m³)			CL (m)			LCR			SCI		
		Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
Fr	P	18.6	24.6 (4.3)	37.1	15.7	65.7 (45.1)	211.8	0.4	0.62 (0.1)	0.79	0.23	0.45 (0.1)	0.76	0.15	0.29 (0.1)	0.51
	M	11.2	20.5 (4.2)	27.8	3	52.0 (31.7)	115.2	0.2	0.52 (0.1)	0.72	0.21	0.50 (0.1)	0.86	0.19	0.32 (0.1)	0.48
Sp	P	14.7	18.3 (2.8)	25.5	6.15	32.9 (20.7)	78.3	0.5	0.62 (0.1)	0.76	0.4	0.56 (0.1)	0.75	0.13	0.23 (0.1)	0.47
	M	9.2	14.9 (3.0)	21	4.2	19.5 (16.0)	52.4	0.3	0.57 (0.1)	0.7	0.32	0.47 (0.1)	0.66	0.15	0.34 (0.2)	0.73
Sw	P	27.8	42.5 (11.8)	66.9	39	273.4 (368.4)	736.2	0.3	0.62 (0.1)	0.8	0.33	0.51 (0.1)	0.79	0.15	0.29 (0.1)	0.49
	M	18.2	36.3 (11.3)	58.1	31.9	287.7 (291.3)	894.1	0.1	0.52 (0.1)	0.74	0.41	0.58 (0.1)	0.85	0.18	0.32 (0.1)	0.53
Ge	P	11.7	18.7 (4.7)	25.8	1.1	28.1 (24.3)	80.2	0.4	0.64 (0.1)	0.84	0.1	0.44 (0.1)	0.65	0.11	0.24 (0.1)	0.46
	M	18.7	25.4 (4.4)	34.6	26.9	106.2 (58.9)	222.8	0.6	0.56 (0.1)	0.9	0.36	0.60 (0.1)	0.79	0.11	0.29 (0.1)	0.51
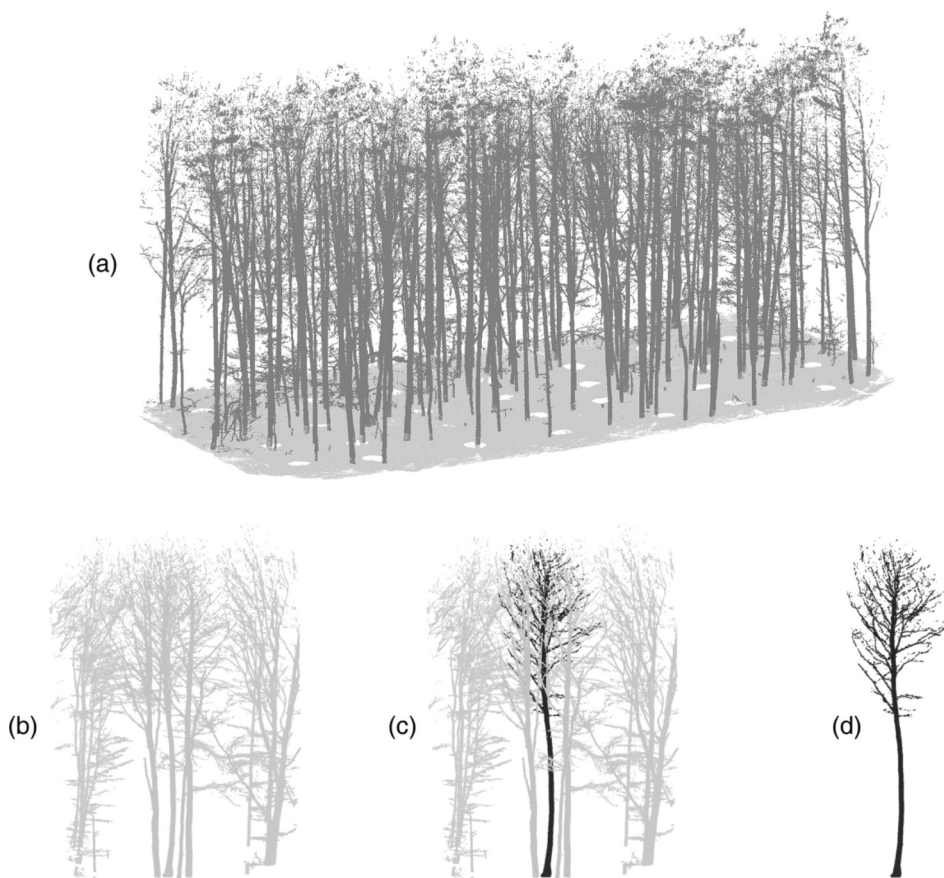
Fig. 3. (a) Point cloud obtained by TLS for one of the studied plots. The empty circles on the ground represent the positions where the scans were taken; (b) subplot centered on the target tree; (c) target tree surrounded by neighbor trees; and (d) segmented target tree.

was obtained by dividing the tree point cloud into 10-cm-thick slices along the vertical axis (Fig. 4). For each slice, the area of the smallest 2D convex hull of the vertical projection of the points from the slice was computed. CV was then estimated by adding the area of each slice multiplied by 10 cm (Fernández-Sarría et al., 2013). As a prerequisite for CV calculation, the height of the crown base was defined as the height of the first slice whose area fell under twice the basal area of the tree, in the downward direction (Metz et al., 2013). Vertical profiles of crown width (CW) were generated for each tree of interest in 10 cm height increments using the radius with the circle with the same area as the area from the corresponding slice. To facilitate comparisons among trees of different CL and TTH, the CL was rescaled between 0 and 1 and the CW was rescaled by dividing it by the CL for each tree following Ferrarese et al. (2015). We also calculated for each tree the maximum crown width (CW_{max}) and the live crown ratio (LCR), which was obtained as the ratio between the absolute value of CL and TTH (Tables 1 and S3). Finally, to examine crown expansion (i.e. the potential role of

branches to horizontally colonize canopy gaps) we calculated the space capture index (SCI) (Fleck et al., 2011), defined as the non-convex hull area of the crown projection which contains all the branches relative to the smallest convex hull area of the crown projection (i.e. with no indentations) (Fig. 4).

The non-convex crown projection area was assessed from polygonal meshing (projecting the crown points on a horizontal plane and linking them with triangles with a maximal edge length of 50 cm) in PolyWorks software. Higher values of the index indicate a higher ratio between both areas, which are related to larger extension of individual branches (Fig. 4).

2.5. Data analysis

In our study, each sample (pure *vs*. mixed) was collected from a single monitoring unit where all of the trees occur within a single plot of each treatment. However, our analysis was replicated at four sites. To
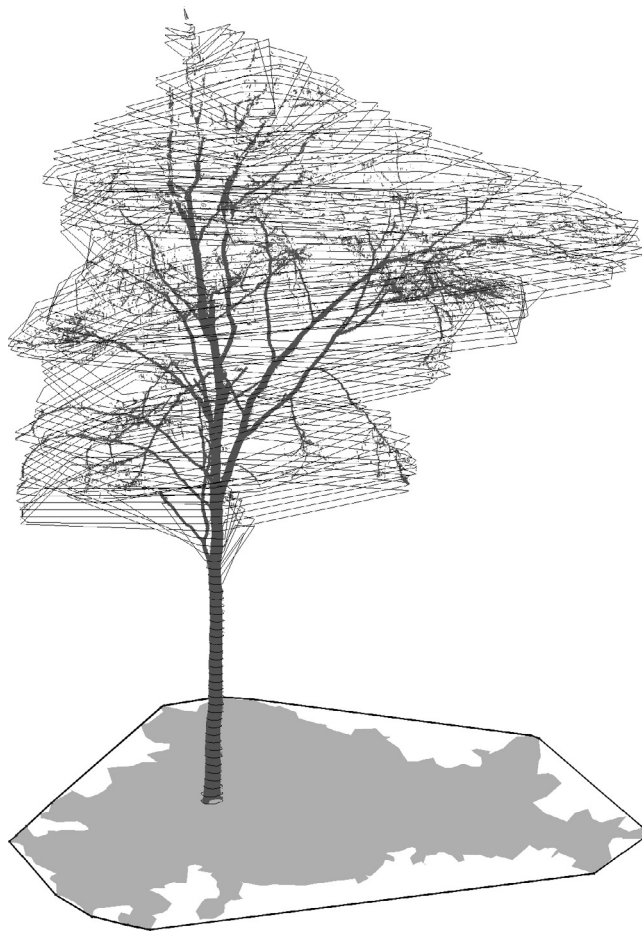
Fig. 4. Point cloud for a single *F. sylvatica* tree. 10-cm wide slices were adjusted to the crown for volume calculation. The SCI (space capture index) is quantified as the non-convex hull projection (shown in gray) relative to the convex hull projection (shown in black).

test if trees in mixture develop larger crowns, we used a base model with tree diameter (DBH) and mixture (as a binary variable, with levels "pure" and "mixed") as predictors of CV based on least squares fits. Separate equations were fitted for each site (Table 2). Both CV and DBH were ln-transformed to reduce heteroscedasticity such that the model error terms are normally distributed ($\varepsilon \sim N(0,\sigma)$). Tree diameter has

been reported as one of the strongest predictors of crown biomass (Affleck et al., 2012). Other tree dimension variables, TTH and CL were tested as predictors because they can account for differences in stand density and relative tree size and have been shown to improve crown biomass models (Mäkelä and Valentine, 2006). Both variables and the interaction effect DBH x mixture were tested but not kept in the models because they were not significant.

To evaluate the statistical differences among the four sites, we fitted a linear mixed-effects model for CV, LCR and SCI pooling together all 160 trees, including stand productivity and its interaction with mixture as predictors, and with site as a random effect to account for within site tree correlation. The CVP index was tested as a predictor but was not kept in the models because it was not significant.

To further explore if trees in mixture develop different shapes of vertical volume distribution compared with those in pure stands, several non-linear models were tested as crown profile (CP) functions and the three-parameter beta function performed the best. Beta curves were fit to pure and mixed stands separately and per site to produce a CP shape (Table 2). For the beta function, β_0 is a scaling term added to fit the x-values of the points when CL was constrained between 0 and 1 and β_1 and β_2 are the distribution shape parameters (see Ferrarese et al., 2015). In addition, following Garber and Maguire (2005) and to test the influence of site productivity on the CP, the beta parameter estimates obtained for each tree were modeled as a linear function of mixture, with DBH and productivity as covariates. Because the three beta parameters were correlated, we modeled them with a system of simultaneous equations using seemingly unrelated regression (Zellner, 1962).

Standardized residuals were visually assessed for all models to ascertain whether any remaining pattern with respect to the explanatory variables was to be found. Final model selection was based on minimum Akaike's information criterion (AIC). In order to evaluate the variability among crown sizes and shapes in both pure and mixed stands, we calculated the square root of the mean square error (RMSE) for the model predictions in each stand composition. For the linear model, alternative models were also compared based on the R^2. All statistical analyses were carried out using R 3.2.1 (R Development Core Team, 2016). For the non-linear models we used the package *nlme* (Pinheiro et al., 2015), and for the seemingly unrelated regression we used the package *systemfit* (Henningsen and Hamann, 2007). We used the *MuMln* package (Barton, 2016) to calculate the marginal R^2 values (R^2_m; those due to fixed effects only) and conditional R^2 values (R^2_c; those due to fixed plus random effects). We also calculated the RMSE for the fixed-effects model ($RMSE_c$) and for the fixed plus random effects ($RMSE_m$).

Table 2

Model parameters for crown volume (CV) and crown profile (CW = crown width; CL = crown length) at each site. The four sites are presented in order of increasing site productivity. Standard errors of parameter estimates are given in brackets. All variables included are significant (p < 0.05). RMSE is in the same unit as the dependent variable.

| Response	Site	Stand type	Model form and parameter estimates			R^2	RMSE
			β_0	β_1	β_2		
Crown volume			$\ln(CV) = \ln(\beta_0) + \beta_1\ln(DBH) + Mixture$				
	Fr		−4.29 (1.18)	2.63 (0.38)	–	0.56	0.50
	Sp		−6.38 (0.94)	3.35 (0.34)	–	0.72	0.43
	Sw		−5.43 (1.17)	2.84 (0.31)	0.52 (0.18)	0.69	0.53
	Ge		−8.85 (1.04)	4.02 (0.36)	0.39 (0.19)	0.87	0.47
Crown profile			$CW = \beta_0 x \frac{CL^{\beta_1-1} \times (1-CL)^{\beta_2-1}}{beta(\beta_1,\beta_2)}$				
	Fr	Pure	0.43 (0.01)	2.71 (0.10)	2.03 (0.07)	–	0.38
		Mixed	0.47 (0.01)	2.75 (0.09)	2.53 (0.08)	–	0.38
	Sp	Pure	0.39 (0.01)	2.82 (0.09)	2.13 (0.06)	–	0.28
		Mixed	0.36 (0.01)	2.51 (0.09)	2.11 (0.08)	–	0.28
	Sw	Pure	1.04 (0.02)	1.87 (0.08)	1.68 (0.07)	–	0.62
		Mixed	1.36 (0.02)	2.16 (0.07)	2.09 (0.07)	–	0.72
	Ge	Pure	0.34 (0.01)	2.78 (0.10)	1.79 (0.06)	–	0.28
		Mixed	0.51 (0.01)	2.16 (0.05)	1.82 (0.04)	–	0.39
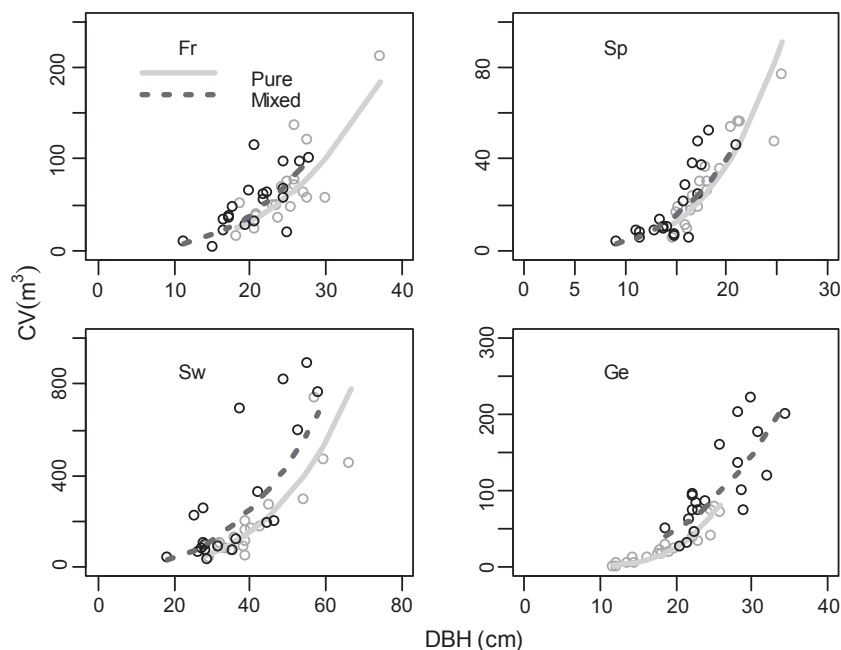
Fig. 5. CV (crown volume) as a function of DBH (diameter at breast height) for *F. sylvatica* trees in pure and mixed stands for the four sites studied. The curves show higher values of CV for *F. sylvatica* for a given DBH in the mixed stands than in the pure stands.

3. Results

As a result of lateral and vertical expansion of the crowns, for a given DBH, *F. sylvatica* trees had higher CV in mixed stands than those in pure stands (Fig. 5). The results of the general model across all sites showed that the effect increased with productivity (p = 0.021; $R^2_m = 0.83$; $R^2_c = 0.86$; $RMSE_m = 0.51$; $RMSE_c = 0.50$), with the mixing effects being significant in the two most productive sites (Germany and Sweden) and non-significant for the two least productive sites (France and Spain).

The variability in CV increased with DBH, especially for the trees in mixtures. As a result, when the models were fitted separately for pure and mixed stands, the variance was lower for the allometric relationships in pure stands at all sites; the lower R^2 were found for models in mixed stands (Table S4). The higher variability in CV for a given diameter was also indicated by consistently higher values of RMSE in the mixtures (Table S4).

LCR and SCI were not influenced by DBH. Mixing did not affect LCR but there was a marginally significant interaction between mixing and site productivity (p = 0.06; $R^2_m = 0.39$; $R^2_c = 0.61$; $RMSE_m = 0.11$; $RMSE_c = 0.10$). In all four sites, mixed stands presented higher maximum values of LCR than pure stands (Table 1; Fig. 6). Productivity did

not significantly affect SCI, and the contribution of the random effect site was negligible ($R^2_m = 0.06$; $R^2_c = 0.06$; $RMSE_m = 0.11$; $RMSE_c = 0.11$). However, mixing significantly increased SCI (p = 0.05) Again, higher values could be observed in the mixed stands vs. the pure stands in Spain except in France (Table 1; Fig. 6). The variability of LCR and SCI, represented by the standard deviation values, was not higher in mixed stands than in pure stands (Table 1).

F. sylvatica trees in mixtures showed a downward shift of volume distribution, with a higher proportion in the lower canopy and the maximal horizontal crown extension shifted to a relatively low height within the crown (Fig. 7); trees in mixed stands presented lower mean and minimum values of CL for the maximum CW at the four sites (Table 1). These differences were more apparent in the two most productive sites (Germany and Sweden; Fig. 7). This was confirmed by the modeled beta parameters of the curves when we pooled all the sites together; the scaling parameter β_0 significantly increased with DBH in all sites, resulting in a relative larger CW_{max}. β_0 was also affected by productivity with lower CW_{max} in the most productive sites ($\beta_0 = -2.15 + 0.9 \times \ln (DBH) + 0.28 \times Mixture - 0.02 \times Productivity$). However, the shape parameter β_1 was unaffected by productivity but significantly affected by the mixture with negative values of β_1 shifting the CW_{max} to relatively lower height values within the
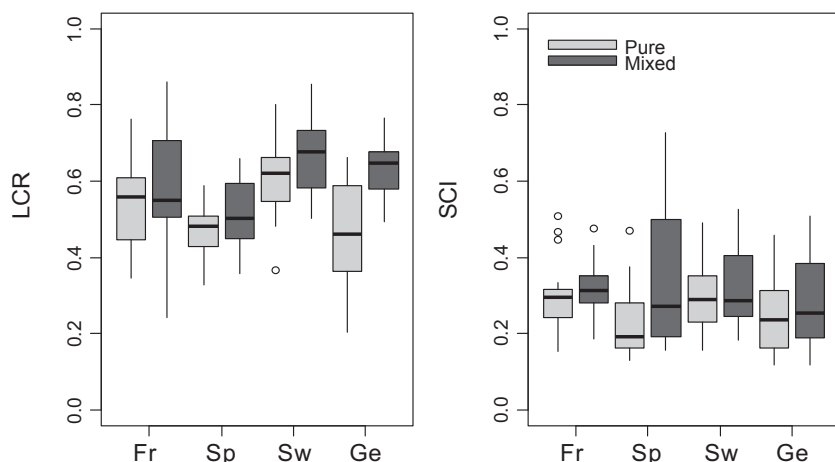

Fig. 6. Live crown ratio (CL: TTH; LCR) and space capture index (SCI) for the four sites in the mixed and pure stands. The four sites are presented in order of increasing site productivity. Higher maximum values and upper quartile values (75% of the data) are observed for LCR and SCI in the mixed stands compared to the pure stands.
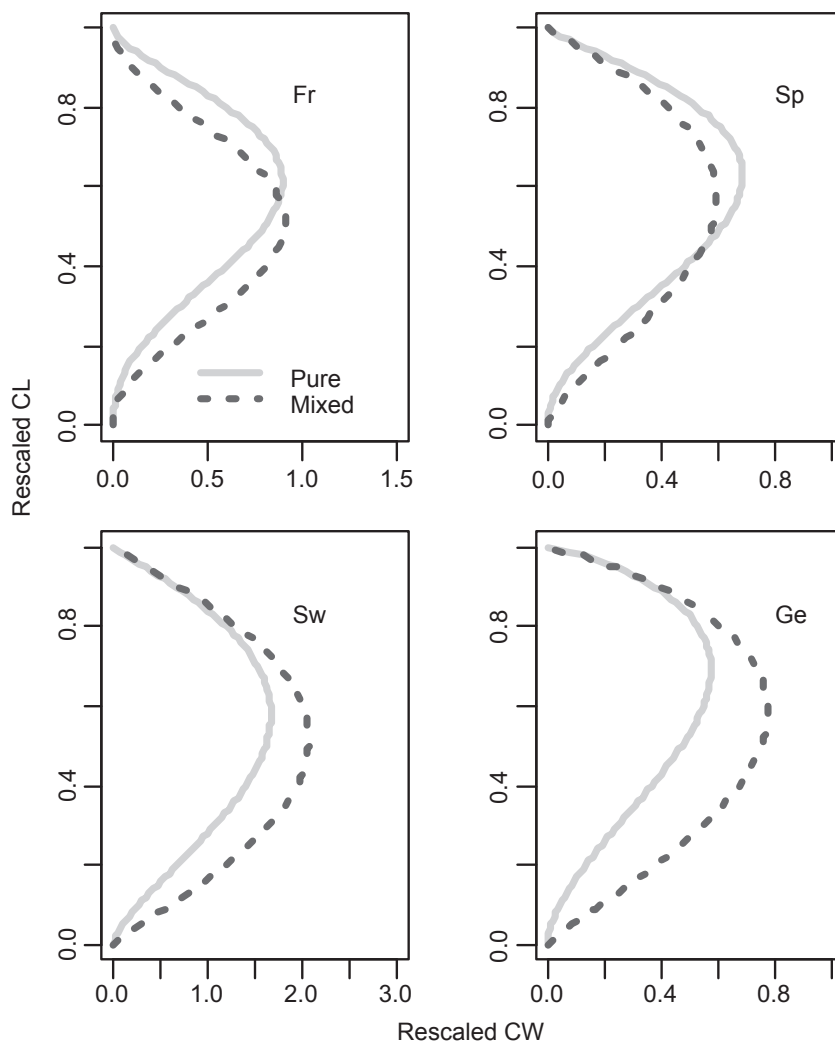
Fig. 7. Beta (scaling parameter-modified) curves modeled on the CW (crown width) of the equivalent circle of each 10 cm slice, after rescaling the CL (crown length; 0–1) and the CW (relative to the CL) for the four sites. The curves show wider and lower-reaching crowns of *F. sylvatica* in mixed stands compared with pure stands.

crown (β_1 = 3.28–0.55 × *Mixture*), while β_2 was not significantly affected by any of the covariates. Although higher values of RMSE were found in Sweden and Germany (Table 1), the standard deviation of the parameters of the beta curves in the four sites did not differ between pure and mixed stands (Table 2).

4. Discussion

We found variation in the crown size and shape of *F. sylvatica* in response to mixing with *P. sylvestris*. The effect was largely maintained across sites, with higher values in the mixed stands for all the crown variables investigated. The magnitude of this difference was variable among the crown metrics investigated but overall it increased in the two most productive sites, supporting our hypothesis.

4.1. Effect of mixture on crown characteristics

DBH was the most important predictor of CV, while TTH and CL were not significant. This is likely a consequence of our sites being fully stocked, because CV models using only DBH as a predictor can be adequate for stands with a narrow range of stand structural conditions (Rouvinen and Kuuluvainen, 1997). Mixed stands yielded larger crown volumes in the four sites compared to pure stands, although mixing was only significant in the two most productive sites (Germany and Sweden) supporting our hypothesis about productivity modulating mixing effects on crown allometry. Our results join previous studies in showing an increase in CV in mixed species stands (Jucker et al., 2015;

Kaitaniemi and Lintunen, 2010; Sapijanskas et al., 2014). Our findings provide evidence that drivers of larger crown volumes are both vertical and lateral expansion of the crowns, as also observed in mixtures with other species (Bauhus et al., 2004; Forrester et al., 2016; Longuetaud et al., 2013). Mixing had a significant effect on crown vertical dimension, with *F. sylvatica* trees developing deeper crowns in mixtures. This effect was also more evident in the two most productive sites, consistent with our hypothesis. Such a shift in crown shape towards a lower center of gravity was also observed for saplings and mature trees of *F. sylvatica* mixed with species that had more rapid height growth (Petrițan et al., 2008; Pretzsch and Schütze, 2005). We found a CW_{max} in a lower position in mixture than in pure stands, which is consistent with results obtained by Bayer et al. (2013) who showed that *F. sylvatica* develops steeper branches in pure stands than in mixtures with *Picea abies* and by Martin-Ducup et al. (2016) who found that the percentage of shade crown relative to CL was higher in *Acer saccharum* pure stands than in mixtures.

Higher values were consistently observed for crown expansion (higher SCI = more indentations, less homogeneous crown shape) in the mixtures, revealing that trees spread sideways in mixtures more than in pure stands, thereby filling the space in a different layer. However, the weak effect of mixture (R^2_m of the model = 0.05) and the small differences in mean values of SCI between mixed and pure stands could be because of the choice of dominant trees, as this difference was shown to be more pronounced in suppressed trees (Fleck et al., 2011). While the size of the crowns changed, there was no difference in canopy packing (total crown volume per canopy volume) between *F. sylvatica*

monocultures and mixtures with *P. sylvestris* along a 21-site transect, which included the plots in this study (Forrester et al. in press). Furthermore, the leaf area density (total leaf area per canopy volume) of the canopy was lower in the mixtures than in the *F. sylvatica* monocultures (Forrester et al. in press). Increasing crown dimensions or shifting crown positions may therefore be a more efficient way to improve light absorption than by increasing canopy density (i.e. the crown or leaf area density of the canopy), because increases in density may also increase self–shading. Similarly, leaf area density tends to change much less than crown lengths and widths in response to many different treatments, including thinning, fertilizer application, and pruning (Forrester et al., 2012; Guisasola et al., 2015; Ligot et al., 2014). Higher or lower values of crown metrics obtained in mixed stands did not always translate into higher crown variability in the mixed stands. This was likely a result of choosing trees mixed on a tree-by-tree basis, not capturing situations with a pure *F. sylvatica* local neighborhood in the mixture. Overall, the difference in the values obtained for the variables describing crown size and shape found in mixtures supported our hypothesis and confirms previous research showing the potential of *F. sylvatica* to plastically respond to changes in canopy conditions by exploring more space in multispecies stands (Longuetaud et al., 2013; Seidel et al., 2011).

4.2. Crown response to mixture across a productivity gradient

The smaller differences observed in crown volume and crown profile in France and Spain than in the two most productive sites are likely related to the less optimal growth conditions of *F. sylvatica* in the least productive sites linked to soil resource availability (Forrester et al., 2016). This is in line with a previous study that found a smaller reduction in crown extension of *F. sylvatica* with increasing site fertility in mixture with *P. abies* (Dieler and Pretzsch, 2013). However, given the lack of significance of the CVP index in our models, and the weak correlation between CVP and mean volume annual growth (used to define productivity) in the 32 sites installed across Europe, including the four in this study (Pearson correlation coefficient, $r = 0.22$), we argue that our proxy for site productivity could be a better predictor of crown differences than CVP because it reflects not only potential growth conditions but also other potential influential factors such as past stand dynamics.

A recent study using a larger sample of the same *F. sylvatica*- *P. sylvestris* triplets found that differences in stand structure increased with water availability (Pretzsch et al., 2016). However, even at sites with similar water availability, crown characteristics could be influenced by repeated droughts causing a substantial loss of biomass (Rasheed and Delagrange, 2016). The magnitude of the mixing effect could also be affected by other factors such as differences in topography, wind exposure or the genetic variability of *F. sylvatica* among sites, although genotypic variation has been found to have a much weaker effect on structural traits than phenotypic plasticity in *F. sylvatica* (Meier et al., 2008; Knutzen et al., 2015).

Our results may also be influenced by the developmental stage studied, since increasing age can modify the vertical separation of the species in the canopy zone (Martin-Ducup et al., 2016; Thurm and Pretzsch, 2016). For this research our sample is limited to dominant trees in dense stands, where interactions between species are more intense and the effects on crown structure are likely more noticeable. Earlier studies that observed larger crowns in mixtures compared to pure stands for a given stem diameter were also in stands where the crowns have had enough time to develop and interact (Bauhus et al., 2004; Bayer et al., 2013; Forrester et al., 2016). However, diversity did not have a strong influence on the crown architecture of *F. sylvatica* in juvenile plantations (Barbeito et al., 2014; Van de Peer et al., 2017). Whether this lack of differences will change over time or may be a consequence of productivity would require long-term observations. Therefore, to understand the contribution of mixtures to differences in

canopy structure, further studies could incorporate 3D crown geometry data to examine how the relative contribution of these factors, together with the species choice, modulate canopy structure.

4.3. Benefits and opportunities of TLS for the study of mixtures

The high morphological plasticity of *F. sylvatica* is well known. However, our work confirms recent studies showing that TLS can improve our ability to quantify this plasticity (Martin-Ducup et al., 2016; Seidel et al., 2011). TLS derived crown metrics for crown structure quantification such as CV or SCI can give further insight on the role that intra- and inter-specific competition have in crown size and shape and can be easily expanded to other species and ecosystems. These variables revealed a site effect on mixing that was not detected with conventional measures such as CL both at our sites and at a larger number of sites, which included the plots in this study (Forrester et al., in press). Such innovative metrics may also contribute to better analyzing, tracing, and modeling the overyielding effects of mixed *versus* monospecific stands often caused by *F. sylvatica* (Pretzsch et al., 2015), and their dependency on higher light interception. The relevance of the observed structural changes detected by the TLS variables for increasing species diversity should also be further evaluated.

Our approach to calculate tree crown volume does not involve any assumption about tree structure and crown shape (Calders et al., 2015) and it could therefore be used to quantify crown changes (Martin-Ducup et al., 2017) and how mixtures enhance the resilience to disturbances over time. In particular, vertical crown profile models developed from TLS hold great potential to monitor and model the effects of disturbances such as ice storms (Nock et al., 2013), needle disease (Weiskittel et al., 2007) or crown fire risk (Crecente-Campo et al., 2009), which are all influenced by vertical canopy structure.

5. Conclusions

We investigated how mixing affects the crown size and shape of *F. sylvatica* across a gradient of productivity conditions in Europe. Regardless of site conditions, generally the maximum observed values of all the crown characteristics investigated of *F. sylvatica* were found in mixed stands. The magnitude of the mixing effect between pure and mixed stands was variable among the crown characteristics investigated, but overall was more significant in the two most productive sites. However, our results are based only on four sites with contrasting productivity. Further investigations including a more continuous gradient of productivity, controlling for other potential influential factors such as past management, topography or genetic variability, would be required to better disentangle the influence of this factor on the differences between canopies in pure and mixed stands. Our study highlights the value of TLS-derived variables that can complement the quantification of intra-specific crown morphological plasticity and reveal spatial changes in mixing effects not captured traditional field methods.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.09.043.

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