Tree species diversity does not compromise stem quality in major European forest types

Adam Benneter[a],[*], David I. Forrester[a],[b], Olivier Bouriaud[c], Carsten F. Dormann[d], Jürgen Bauhus[a]

[a] Faculty of Environment and Natural Resources, Albert-Ludwigs-University Freiburg, Germany
[b] Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland
[c] Stefan cel Mare University of Suceava, Faculty of Forestry, Suceava, Romania
[d] Department of Biometry and Environmental System Analysis, Faculty of Environment and Natural Resources, Albert-Ludwigs-University Freiburg, Germany

ARTICLE INFO

ABSTRACT

Mixed-species forests can have higher productivity, in terms of wood volume, than monospecific forests. In addition, higher tree species richness has been found to positively correlate with multiple ecosystem services and functions. Surprisingly, stem quality as one of the most important factors regarding the economic value of forests has rarely been formally studied in diverse forests. This paper aims at investigating how tree species richness influences stem quality and which factors may drive quality development in these stands. Stem quality, understood here essentially as the suitability of a particular stem for particular end-uses, is influenced by a tree's ability to capture sufficient resources for growth and is influenced by neighbouring trees, e.g. through shading and physical crown interactions. We collected data on crown size, stem form and tree health for over 12,000 trees in 209 study plots in six European regions (Finland, Germany, Poland, Romania, Italy and Spain) within naturally diverse forests to assess the impact of tree species richness on these characteristics. Results showed that quality variability between regions, stands and individual trees was high across species. At the stand level, there was a slight tendency towards lower stem quality with increasing diversity. However, individual trees of high quality were present at all diversity levels and for all target species. Tree species richness could not be confirmed as a primary influence on stem quality at the stand level. Rather, stand and individual tree properties such as structural composition, competition, tree size and crown characteristics were identified as the main factors for stem quality development, even in mixed stands. Many of the factors identified in this study can be directly or indirectly influenced by forest management strategies tailored to produce high-quality timber in mixed-species forests. Our findings suggest that diverse stands are not inferior regarding stem quality, while at the same time being able to provide various other ecosystem services.

1. Introduction

There is now a large body of evidence that tree species diversity has in most cases a positive influence on the biomass productivity of forest ecosystems (Bauhus et al., 2017; Forrester and Bauhus, 2016; Liang et al., 2016; Paquette and Messier, 2011; Pretzsch et al., 2015; Ruiz-Benito et al., 2014; Vilà et al., 2013). Tree species diversity may also enhance the provision of other ecosystem services, such as water purification, air cleansing and oxygen provision, soil development and retention, regional climate regulation and carbon sequestration (Cardinale et al., 2011; Gamfeldt et al., 2013; Noss, 2001; Ozanne et al., 2003; Ruiz-Jaen and Potvin, 2011). Surprisingly though, the main interest of many forest owners *besides* biomass productivity – namely the commercial value of forest production – has remained largely

unaddressed in biodiversity research in forests (Knoke, 2008). While the other mentioned ecosystem services may have economic relevance, they cannot be marketed unless some ethical and structural issues can be resolved. Presently, the marketing of only these services does not offer promising economic opportunities for most forest owners (Muradian et al., 2013). Until they do, the prime direct economic function of forests is based on the production of wood. Consequently, if forest owners are to adopt management systems comprising higher tree species diversity, they must be convinced that this improves not only societal values but also their income and the economic value of their forests. If tree species diversity can enhance biomass productivity, forest owners and managers producing timber for low-value end-uses, such as pulp and paper, fibre boards and fuel certainly can profit from managing for higher diversity. But while these products make up a large

portion of the total wood consumption, profitable forest management depends on production of high quality timber in many parts of the world. Therefore, biomass productivity alone is not sufficient for economic valuation of most forests. Market prices of logs for high-revenue end-uses, such as appearance-grade lumber and veneer, depend strongly on the quality of the raw material – timber. Forest owners will thus only be willing to manage forests with higher tree species diversity, if this improves, or at least does not compromise, the production of high quality timber.

One might argue, that unlike quantity, quality "lies in the eye of the beholder", or in the case of timber, is determined by the motives of the utiliser of the final wood product. It has therefore been proposed to define timber quality according to its intended end-use (see for example van Leeuwen et al. 2011). For the timber provider, however, two problems arise from this approach.

Firstly, it is difficult to find one single measure to satisfy the information need about the quality of the resulting roundwood log, let alone that of the lumber, as long as the tree is still standing.

While it would be ideal to know the intrinsic properties of the resulting roundwood or lumber products while trees are still standing, these properties are costly and onerous to study, because sampling is in most cases destructive. It is hence necessary to already gain a reasonable insight about the quality of trees and stands even when the final harvest is decades away. Therefore, forest managers must rely on extrinsic, or external, quality assessment proxies to decide about the retention or the removal of trees during management operations.

Secondly, even if all information was available before the trees were harvested, limiting the production of a given stand to only one end-use can be risky and problematic, even in plantations, where this has historically been considered less of a problem (Kelty, 2006; Piotto et al., 2010). Therefore, managers must operate with a grading system that provides them with some flexibility in terms of end-uses. A stem with prospective veneer-quality (typically the highest quality grade) can be used for a cascade of lower-grade end-uses if its quality deteriorates over time.

These external stem properties are indicated by the presence of branches, knots, branch wounds and stem deformations, curvature, taper, epicormic branching, and defects caused by mechanical damage, irregular growth, pests and pathogens (Dănescu et al., 2015; Larson, 1963; Mäkinen, 1999; Thies et al., 2004). Many of these properties may be influenced by the tree species composition of stands. In mixed stands, for example, branchiness may be increased, because trees of different species often exhibit different light transmission (Dong et al., 2016; Medhurst et al., 2003). This can lead to certain trees developing more branches in spaces with higher irradiation (Forrester et al., 2012).

Even though stem quality, as judged by these external variables, is not linearly related to roundwood and lumber quality, a tree with high stem quality is more likely to yield roundwood and sawnwood of high quality than one with low stem quality (Sterba et al., 2006).

In order to provide an effective assessment scheme, stem quality in forestry has been traditionally defined using classes such as A, B, C, D grade (e.g. European Commission, 1997, 2008), especially for hardwoods. These allow the timber provider a relatively simple allotment of the timber and give prospective buyers a reasonably accurate prediction of the degree to which the timber fulfils certain wood property requirements by specifying thresholds for stem defects (i.e. deviations from the properties of a log considered nearly flawless, or of grade A). The differences in economic terms between these classes can be considerable (see for example Supporting Information S1-1, Table S1-1).

In forestry, knowledge about the effect of tree species interactions on timber quality is largely restricted to specific mixtures in which at least one species is used to facilitate quality development in at least one other species, for example the facilitation of self-pruning on the lower stem of valuable hardwoods through subdominant shade-tolerant species (Burschel and Huss, 1997; Kramer, 1988; Röhle, 1984; Saha et al., 2014; von Lüpke, 1998). In contrast, the development of timber quality

in even-aged monocultures has been intensively studied for many commercially important species (e.g. Erickson and Harrison, 1974; Medhurst et al., 2011; von Lüpke, 1998; Zobel, 1984). Yet, there is very little general information on timber quality in mixed-species stands (Bauhus et al., 2009, 2017). Mixtures tend to provide more heterogeneous growing conditions owing to differing growth dynamics, morphology, and ecological adaptations of the participating species (Pretzsch and Rais, 2016). This structural heterogeneity may increase the variability in stem and crown properties such as taper, straightness or stem and crown form regularity of all or some species in the mixture (Jucker et al., 2015; Pretzsch, 2006).

Mixtures of species with differing crown architecture and apical dominance may also exhibit more curved and leaning trees, if one species is forced to grow into unoccupied or unshaded growing space to compete for light, exhibiting phototropic growth (Grotta et al., 2004), or if species with strongly different resistance to mechanical branch abrasion (Hajek et al., 2015; Putz et al., 1984) are mixed. This may also lead to irregular crown shapes and associated variable branch dimensions, where branches exposed to more light and growing space are longer and thicker (Kint et al., 2010). Differences in light transmittance between species may also promote epicormic branching in areas with higher light exposure compared to more homogeneous monospecific stands (Blum, 1963; Books and Tubbs, 1970; Takiya et al., 2010).

The competitive influences of the direct tree neighbourhood, along with the species-specific architectural traits and the site influences, shape the morphology and growth dynamics of a given target tree (Lang et al., 2010; Ratcliffe et al., 2015). Neighbourhood-level analyses, therefore, promise important insights into species diversity influences on stem quality. But while single-tree-based silvicultural approaches are gaining importance, especially in forests managed for multiple services and high stem quality, the stand level often remains the central scope for mid- and long-term planning, yield and revenue calculation and inventory and implementation assessment (Oliver and Larson, 1990; Pukkala, 2002). In addition, tree species diversity of forests and the degree and form of mixture, are commonly understood as stand-level variables by managers and their impact is often evaluated at that spatial scale (Kuuluvainen, 2009; Pretzsch and Schütze, 2009). Consequently, we analysed stem quality in this study at the level of the stand and aggregated important variables at the stand-level. While there is some knowledge on the effects of specific tree species interactions, there is no general information on how stem quality of trees may change with increasing tree species diversity (Bauhus et al., 2017). Therefore, our study addressed the hypotheses that:

(1) tree species richness affects crown and canopy characteristics, which are responsible for stem quality development, and
(2) the quality of tree stems is negatively related to tree species richness

To analyse the relationship between tree species diversity and stem quality, we used forest stands covering a wide range of tree species combinations in different climatic and vegetation zones across Europe.

2. Materials and methods

2.1. Study design

To study the effect of tree species diversity on stem quality, we used plots ranging in tree species richness from 1 to 5 species for a variety of combinations of European tree species from boreal to Mediterranean forest ecosystems. The study areas and plots were the same as used in the interdisciplinary project FunDivEurope (http://www.fundiveurope.eu/) (Baeten et al., 2013). The exploratory platform of this project offered a wide geographic and climatic range, and a pool of tree species representing Europe's economically most important species (see S1-3 in Supporting Information 1 for a full list of species, species compositions

and plot data). The project's exploratory platform covers six European forest types and bioclimatic regions, from boreal forest in Finland, hemiboreal forest in Poland, mixed beech forest in Germany, montane mixed beech forest in Romania, thermophilous deciduous forest in Italy to Mediterranean mixed forest in Spain. Each region comprised between 28 and 43 plots of 30 × 30 m in mature forests (208 plots in total). The plots were selected so that target species were present at all species richness levels within a region (Finland 1–3 species; Germany, Romania and Spain 1–4; Italy and Poland 1–5) and that each tree species composition was replicated at least twice. Also, evenness of tree species was kept as high as possible by making sure that target species had similar abundances within mixtures with a lower limit of 60% of maximum evenness based on basal area proportions. In addition, spatial autocorrelation was avoided where possible by choosing a minimum distance between plots of approximately 100 m, while ensuring that plots were comparable in topography, soil type and management history. While all species compositions were representative of a major forest type in the respective region, some species occurred in more than one region (e.g. *Acer pseudoplatanus, Fagus sylvatica, Picea abies, Pinus sylvestris*). All target tree species were canopy species. In some forests, it was impossible to find mixed-species stands comprised exclusively of the target species. However, all non-target species within the plots were sub-canopy species and were not used in our analyses. For more detail on the design see Baeten et al. (2013).

2.2. Stem quality score

To assess the influence of tree species diversity on stem quality for each plot, dendrometric data such as tree diameter, tree height and height of the lowest live branch, and externally visible stem characterics were recorded. The silvicultural quality assessment was based on stem characteristics that can be measured and evaluated non-destructively and rapidly along with a measurement of possible influencing factors at the tree and stand level. Even though the definition of timber or stem quality attributes is partly species-specific (Knoke et al., 2006), most commercial species share a set of indicators for the most important stem quality properties. Assuming the tree is healthy, the presence or absence of branches (and to a degree of epicormic branches) in the lower stem section is among the most important quality properties, followed by stem sweep and defects (European Commission, 1997, 2008a; Hein, 2009; Kint et al., 2010; Kuehne et al., 2013).

Therefore, we concentrated our assessment on the following variables: 'stem quality' class, 'branch-free bole-length', 'stem curvature' and 'epicormic branching'. A description of these variables and justification for their selection is given in Table 1.

Owing to the many factors constituting stem and wood quality, a four-class grading scheme was used to combine the total number of stem quality variables collected for each tree into an appropriate 'stem quality' score. This enabled us to analyse a single response variable across all regions, species diversity levels and compositions (see Table 1

and Supporting Information S1-1 for details). For each tree, diameter at breast height, species identity, tree height and height of the crown base (HCB) was measured.

2.3. Assessment of competition

To account for the influence of competition, we calculated two indices (Forrester et al., 2017). The first one was based on the average wood density (Chave et al., 2009) of each species. The second one was based on the relative shade tolerance of each species, taken from (Niinemets and Valladares, 2006).

$$I\, d = \sum_i\ (d^2 \times h \times \sigma) \tag{1}$$

$$I\, s = \sum_i\ (d^2 \times h \times s) \tag{2}$$

where I = competition index, i = plot ID, d = diameter at breast height, h = tree height, σ = wood density [kg m^{-3}], s = relative shade tolerance.

Since no value for *Quercus faginea* is reported therein, we used the shade tolerance value of *Quercus ilex* (Sánchez-Gómez et al., 2006). Our reasoning behind the indices was that given a certain wood density, or shade tolerance, a tree's volume expresses its competitive capacity, while inter-specific differences in competitive capacity are correlated with wood density or shade tolerance (Forrester et al., 2017; Kunstler et al., 2016). Since we were interested in the overall competitive pressure within each plot, we summed up the values of each tree's approximate stem volume multiplied by the tree's value of (1) species average wood density or (2) relative shade tolerance.

Crown base was defined as the height of the lowest live primary branch. A widely used 5-class crown dominance classification system based on Kraft (1884) was applied. All measurements were completed between March and October 2012.

2.4. Analytical framework

We used plot-level and tree-level field data, aggregated at the plot level, to model mean plot-level stem quality, mean plot-level branch-free bole length and bole ratio, plot-level occurrence of stem curvature and epicormic branching across 15 target species, 95 species compositions and 6 study regions.

We fitted linear mixed models in which we related tree species richness and several other predictor variables to mean plot-level quality for a total of 208 plots across the six study regions and a total of 15 commercially important tree species. The mean plot-level quality was estimated as the arithmetic mean of the tree-level scores for all trees sampled in a plot, ranging from 14 to 224 trees per plot (Median = 55). In total, 12,302 trees were graded. Details on plot and tree-level data and the grading scheme can be found in Supporting Information 1. Tree

Table 1
Stem quality classification used for this study derived from official roundwood sorting norms of the EU and quality grading guidelines for standing timber developed for the German National Forest Inventory.

Quality class	Conifers	Broadleaved	Source
A = 4	One or more 5 m logs pruned or branch free; no curving; very few epicormics, very few to no pathologic defects; no waviness; no fissures/cracks	A: minimum of 5 m log almost branch-free, very small and few epicormics or branches; no curving; no pathologic defects; no waviness; no fissures/cracks	(European Commission, 1997, 2008a, 2008b; Mahler et al., 2001)
B = 3	One 5 m log almost branch free, few small epicormics; minor 1-sided curve acceptable, little taper; no mistletoe; minor pathologic defects; minor ovality; few branches	One or more 2 m logs largely branch free, no branches over 10 cm, few small epicormics; 1-sided curve acceptable if otherwise acceptable; minor pathologic defects if wood damage is minimal; minor stem ovality; few branches	
C = 2	Large branches along stem; curving, stem wounds, bumps, epicormics accepted	Large branches along stem; curving, stem wounds, bumps, epicormics accepted	
D = 1	Stems are utilizable but are likely to yield less than 40% usable timber	Stems are utilizable but are likely to yield less than 40% usable timber	

species richness used in these models was based on the target species identified at the beginning of the project (see Supporting Information S1-3). All models were also tested with another commonly used measure of diversity (Shannon-Index based on (a) tree species number, (b) tree species basal area both for target species and all species present, respectively), but none of these significantly improved the models in terms of explained variance. For the final models, we used species richness based only on the target species. Tree species not belonging to this pool were excluded from the calculations of species diversity or richness (see Supporting Information 1 for a species list and detailed description in Baeten et al., 2013). These models were not species-specific, and focused on testing the hypothesis that in diverse forest stands, the general mean plot-level quality decreases with higher tree species richness.

The overall design can be described as a nested design, with trees nested within plots, which were nested within regions and species richness measured at the plot level. Because we aggregated the response variables and the predictor variables at the plot level, we introduced region, and not plot, as a random effect. We also included plot-level tree species composition, a factor with 95 levels, as a random effect to correctly identify the variance introduced by this component versus tree species richness. Since composition was neither fully nested nor fully crossed within/across region, we formulated the two random effects as partially crossed/nested (Bolker et al., 2009). After finding that random slope models for each of the numeric fixed predictors did not yield any improvement over random intercept models, we chose to use the latter.

For our analyses, we used the statistics software suite R (R Core Team, 2015) and for the plot-level models, the procedure *lmer* from the *lme4* package (Bates et al., 2014). Mixed-effects models are more robust and flexible than ordinary least-squares (OLS) regression when applied to multi-levelled and crossed/nested designs and non-controllable factors and allow for the inclusion of random effects in order to test for between-group differences that could otherwise be falsely ascribed to fixed variables (treatment) (Bolker et al., 2009). Model comparisons were done based on the Akaike Information Criterion (AIC, Akaike, 1974), likelihood-ratio-tests, and pseudo-R^2 for each candidate model. The pseudo-R^2 was calculated with the function *r.squaredGLMM* in the package *MuMIn* (Barton, 2015). It produces values for marginal and conditional R^2. The marginal R^2 is similar to the R^2 (coefficient of determination) used in ordinary least-squares regression and indicates the variance explained by fixed factors only, while the conditional R^2 indicates the variance explained by both the fixed and random effects in the model.

We first formulated baseline models which related the plot mean of the four individual tree quality variables ('quality score', 'branch-free bole-length', 'curving occurrence' (or 'curvature') and 'epicormic branch occurrence') to tree species richness as the principal explanatory variable. Geographic Latitude of the plots was also included in order to test for an eco-climatic gradient. Latitude was excluded from the models for 'branch-free bole length', 'curvature' and 'epicormic branches', as it did not improve those. The six regions differ in multiple aspects, such as climatic conditions, species pool, management history, soil conditions, topography and several others. Our aim was to test the consistency of the relationship between tree species richness and stem quality across regions. If it was consistent, this would mean that a true species richness effect could be detected, or at least one that holds true for different environmental and forest management conditions. As the data for the two response variables 'epicormic branches' and 'curvature' were between 0 and 1 (absence/presence), we tested whether beta-regression yielded different results to the linear mixed-effect model approach. The beta-regression did not yield fundamentally different results (Supporting Information S1-7, Tables S7-1 and S7-2). Therefore, we used mixed-effect models for these data, because the inclusion of random effects is mandated by the research design and improved the models, the assumptions for linear modelling were satisfactorily met

and interpretation and statistical power of linear models were deemed to be more promising.

2.5. Stem quality variables

Since the proportion of explained variance of the models with only tree species richness as a predictor was low (R^2: Quality score – 0.019, HCB – 0.009, Curvature – 0.002, Epicormics – 0.287) for each of the models (see Supporting Information S1-6, Table S6-2), and none of the relationships between tree species richness-levels and the response variables were significant (all p > 0.09, alpha = 0.05), we subsequently introduced single-tree variables (aggregated at the plot-level, e.g. competition, tree size, crown dominance, crown roundness, tree lean) to test their effect in relation to regional, compositional and tree species richness effects. We also tested environmental variables, such as soil type, soil depth, slope and aspect. While they yielded some improvement over the baseline models, these parameters were dropped from the expanded final models during the model selection stage (see Supporting Information S1-5, Tables S5-3 & 4). To account for confounding effects of different management histories, we also tested simple categorical management-related variables (stand origin, current management), but found no significant effects of these, mainly because these variables were strongly confounded with region and the models were deemed unreliable (see Supporting Information S1-5).

2.6. Fitted models

The final model for plot-level 'stem quality' was

$$MQ_i = \beta_0 + \beta_1 TSR_i + \beta_2 \bar{d}_i + \beta_3 CDC_i + \beta_4 CR_i + \beta_5 CRA_i + \beta_6 LAT_i + \varepsilon_i^a + \varepsilon_i^b \tag{3}$$

where i = plot ID; MQ = plot arithmetic mean of all trees' quality scores; TSR = tree species richness; $\bar{d}$ = plot mean diameter at breast height; CDC = crown dominance class (1 = dominant, 5 = suppressed); CR = the degree of deviation of the horizontal crown outline from a circle on a scale from 0 = fully oval to 1 = fully circular; CRA = crown length divided by total tree height; LAT = plot latitude in decimal notation. ε_i^a and ε_i^b are the random effects terms for region and for species composition at plot level.

For the response variables 'branch-free bole length', 'curvature' and 'epicormic branching' we essentially employed the model-building procedure described above. The model with Curving occurrence as the response variable included a significant two-way interaction term (×) between the percentage of leaning stems per plot and clade (angiosperms, gymnosperms, mixed). The model for 'epicormic branching' included a significant two-way interaction term for species with stem ratio (ratio of total tree height and the 'branch-free bole-length') and clade.

$$MBFB_i = \beta_0 + \beta_1 TSR_i + \beta_2 \sqrt[2]{CISt_i} + \beta_3 CR_i^2 + \beta_4 CDC_i + \beta_5 HDR_i + \varepsilon_i^a + \varepsilon_i^b \tag{4}$$

where i = plot ID; MBFB = plot mean of all trees' branch-free bole-length; TSR = tree species richness; CISt = competition index based on shade tolerance; CDC = crown dominance class (1 = dominant, 5 = suppressed); HDR = the ratio of the total height and the DBH. ε_i^a and ε_i^b are the random effects terms for region and for species composition at plot level

$$PC_i = \beta_0 + \beta_1 TSR_i + \beta_2 \bar{d}_i + \beta_{3,4,5} LEAN_i \times CLADE_i + \varepsilon_i^a + \varepsilon_i^b \tag{5}$$

where i = plot ID; PC = proportion of curved trees per plot in percent/10; TSR = tree species richness; $\bar{d}$ = plot mean diameter at breast height; LEAN = proportion of leaning trees per plot in percent/10; CLADE = species group (conifer, broadleaved, mixed). ε_i^a and $\epsilon \varepsilon_i^b$ are the random effects terms for region and for species composition at plot level

$$PEB_i = \beta_0 + \beta_1 TSR_i + \beta_2 \overline{d}_i + \beta_{3,4,5} SP_i \times SR_i + \beta_{6,7} SP_i \times LEAN_i + \beta_8 CIwd + \varepsilon_i^a \tag{6}$$

where i = plot ID; PEB = proportion of trees with epicormic branches per plot in percent/10; TSR = tree species richness; d = plot mean diameter at breast height; SP = tree species; SR = the ratio of the branch-free stem length and the total tree height, LEAN = proportion of leaning trees per plot in percent/10 and CIwd = competition index based on wood density. ε_i^a is the random effect term for species composition at plot level.

For all models, we visually inspected residual plots (see Supporting Information S1-4, Figures S4-1 & 2), which did not show any obvious deviations from homoscedasticity or normality of error distribution for the full models. We further controlled for collinearity within all models by calculating variance inflation factors using the package *car* (Fox and Weisberg, 2011) and excluded one within each pair of highly collinear variables (e.g. diameter and tree height). We further visually inspected residual variance between categorical variable levels (richness, region and composition) as well as for numeric predictors for homogeneity. The chosen random effects (region and composition, or composition only for the 'epicormic branching' model) were graphically checked regarding confidence intervals and the mean for each of the random effects levels with caterpillar plots to check for deviations from normality of the random effects (see Supporting Information S1-4). To illustrate the effect of region and richness in combination with the stand-level tree attributes, we graphically represented these using individual linear model fits alongside the overall mixed model fits.

In order to complete the analysis and to scrutinise the validity of the conclusions drawn from the models that were not species-specific, we developed a model taking into account species identity for several commercially interesting species. For this, we aggregated the individual-tree variables for each species at the plot level and included predictors showing promise from the above models, employing a corresponding model building and variable/model selection procedure as described above. The species chosen for this analysis were two maple species (*A. pseudoplatanus, A. platanoides*, pooled), *F. sylvatica, F. excelsior, P. sylvestris, P. abies*, the Mediterranean oaks (*Q. cerris, Q. faginea, Q. ilex*, pooled), and the Central European oaks (*Q. petraea* and *Q. robur*). The model formula and output can be found in (Supporting Information S1-6).

To validate our finding that species richness played only a minor role for stem quality at the plot level, we assessed the four models regarding their statistical power. In addition, we assessed the probability that the effect sizes from our models reflected a reasonably reliable estimate of the true magnitude of species richness effects. This would mean that our models were in fact able to capture an approximation of the true effect size of species richness (or that the true effect size is even smaller) and that the effect of species richness is indeed minor compared to other investigated factors. The R code used to conduct this analysis can be found in Supporting Information 2.

We made extensive use of several additional packages for R, including *lmerTest* (Kuznetsova et al., 2014), *nlme* (Pinheiro et al., 2015), *data.table* (Dowle et al., 2014), *reshape2* (Wickham, 2007), *gridExtra* (Auguie, 2016), *sjPlot* (Lüdecke, 2015), *ggplot2* (Wickham, 2009) and *directlabels* (Hocking, 2013).

3. Results

3.1. Average stem quality per plot

The proportions of 'stem quality' classes differed notably across the six study regions (Fig. 1). In all regions, very few stems were found to be of the highest quality. The two Mediterranean regions (Spain and Italy) had the highest proportion of low and low-to-medium quality trees. Poland, Romania and Germany had the most favourable growth

conditions, expressed in absolute tree heights, and had the highest absolute number of stems in high-to-medium and high-quality classes. In Finland, the two medium quality classes were most prominent.

Tree species richness did not show a strong effect on the mean stem quality at the plot level across all regions and compositions (Fig. 2 a) with all species pooled at the plot level. In fact, all variables except for tree species richness showed a significant influence on plot mean stem quality (Table 2) and the model predicted the quality class distribution across tree species richness levels fairly accurately, as indicated by the comparison of actual measured quality scores and quality scores predicted by the model (Supporting Information S1-4, Figure S4-3a). Considering the estimates from the full model, the differences between richness levels were not significant, with very small effect sizes compared to those of other predictors (Table 3). In addition, we were able to show that the highest plot mean quality-scores were obtained in stands with higher proportions of large trees, of trees with rounder, shorter crowns (between 35 and 45 percent crown ratio) and of trees with higher mean crown dominance classes (Table 3 and Table 2). None of these relationships were strongly influenced by tree species richness (Fig. 3), whereas differences between regions were more pronounced (Supporting Information S1-4, Figure S4-5 a), as was also illustrated by the trend towards higher quality from Southern to Northern Europe (Table 3). The random intercept coefficients for different compositions varied only moderately (SE = 0.046, with residual SE = 0.178), indicating that the model captured influences of composition accurately and that the explanatory strength of the fixed terms in the model was largely unaffected by species composition. The random intercept coefficients for region varied more widely (SE = 0.080). Since the mean for Germany deviated from the normality criterion (Supporting Information S1-4, Figure S4-4), we concluded that accounting for this through the random intercept term for region improved the predictive ability of the model.

3.2. Branch-free bole length

Tree species richness alone explained nearly no variance in branch-free bole length (= stem length) per plot in the baseline model (marginal Pseudo-R^2: 0.009, Supporting Information S1-6, Table S6-2). There were notable differences between regions with the lowest average stem lengths in Spain, followed by Italy and Finland and the highest stem lengths in Romania, followed by Germany and Poland (Supporting Information S1-4, Figure S4-5). Branch-free bole length was significantly higher in plots with higher competition, measured as the competition index based on shade tolerance, and ranged from 0 to 2.5 m in the plots with lowest competition to over 15 m in plots with high competition (Fig. 4a), across all richness levels. There was a uniform trend of this relationship across regions. Only for Finland, we found a negative relationship between competition and stem length (Table 2). Branch-free bole length was also related to crown roundness in a curvilinear fashion, such that stem lengths first increased with the average crown roundness, but then declined with crown roundness values nearing perfect circularity. Regional differences and differences between richness levels were minor and not significant for this relationship. The average crown dominance class was a strong predictor for branch-free bole length across regions and richness levels (Table 2). Here stem length declined with decreasing dominance class by approximately 5 m from the highest to the lowest class (Table 3). Again, differences between regions were much more pronounced than between richness levels. Branch-free bole length also increased with average height-diameter-ratio, or slenderness, with consistent trends for region and richness (Fig. 4 b), and differences of almost 11 m between the most tapered and the most slender stems. The random intercept terms for composition and region improved the model significantly over ordinary least-squares regression models, as indicated by the deviations from normality for Spain and several compositions (Supporting Information S4, Figure S4-4).
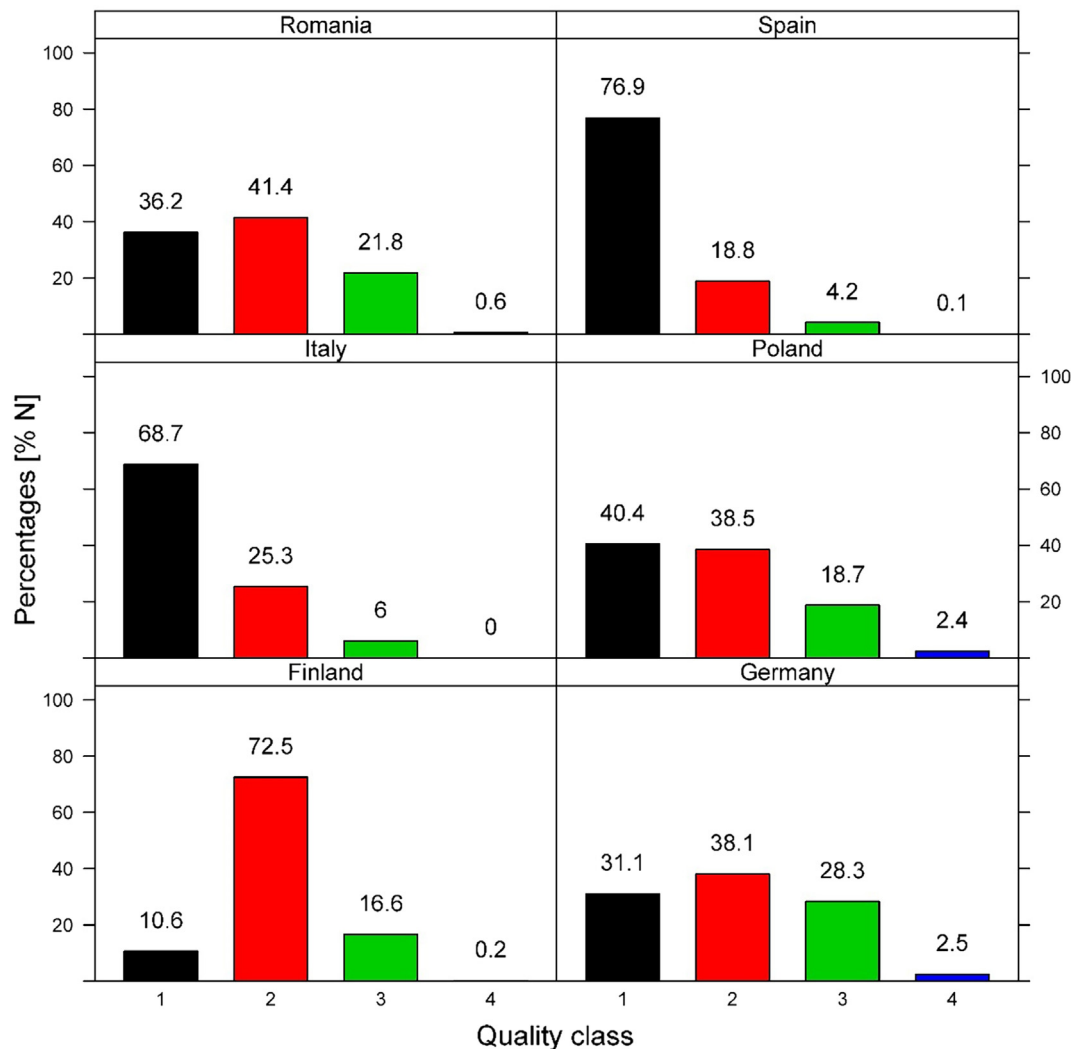
Fig. 1. Stem quality distribution by richness levels and regions. Stem quality classes range from 1 (lowest) to 4 (highest), percentages. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.3. Stem curvature

In the baseline model for 'stem curvature', tree species richness explained almost no variance (marginal Pseudo-R2: 0.002). There were pronounced differences between regions regarding the number of curved stems per plot (Supporting Information S1-4, Figure S4-5), with Italy showing the highest percentage of curved trees (median = 81%), followed by Spain (72%), Germany (68%), Poland (56%), Romania (50%) and Finland (40%). The occurrence of 'stem curvature' was negatively related to average tree diameter, which held true for all regions, albeit to varying degrees illustrated by the different slopes, and across all richness levels (Table 3, Fig. 5 a). It was also strongly related to the occurrence of leaning stems within a plot and the functional group, or clade (angiosperms, gymnosperms), as well as the interaction between these. Monospecific broadleaved stands showed a notably higher proportion of curved trees (50–100%,), than conifers (0–75%,), while in the conifer-broadleaved-mixed stands, the range was intermediate, (25–75%). The association between the occurrence of stem lean and 'curvature', however, was consistent with very similar slopes across regions and clades (Table 3). The consistency of this relationship was even more distinct when comparing the lean-curving-relationship across richness levels (Fig. 5b). While the lack of overlap of the standard errors for some levels of the two random effects with the mean indicated that these situations were not well captured by the full model

fit (see Supporting Information S1-4, Figure S4-4 e, f), we concluded that for most random effect levels, the full model fit was indeed accurate. This suggests further that the inclusion of the random terms improved the models significantly.

3.4. Epicormic branching

We limited our analysis to the following species, because not all species in the full species pool are known to produce epicormic branches: *A. alba, A. pseudoplatanus, C. betulus, C. sativa, F. sylvatica, F. excelsior, O. carpinifolia, Q. cerris, Q. faginea, Q. ilex* and *Q. robur.* Epicormic branch occurrence was aggregated at the plot level for these species and modelled using a similar model structure as for the other quality variables. Epicormic branch occurrence decreased with increasing tree species richness, although overall not significantly (pairwise level comparisons all p > 0.171, Fig. 2d). There were also regional differences (Supporting Information S1-4, Figure S4-5), with Spain showing the highest prevalence of epicormics (median = 56%), followed by Germany (51%), Italy (50%), Romania (39%) and Poland (28%). Differences between richness levels within each region varied, but were significant for Italy (richness levels 2, 3, 4, all p < 0.027) and Spain (richness levels 3, 4, all p < 0.041), suggesting that quality in these regions may have benefited from higher species richness (Supporting Information S1-4, Figure S4-5). There was no consistent

Fig. 2. Boxplots of model predictions for tree species richness (1 = red, 2 = blue, 3 = green, 4 = purple, 5 = pink), for the four models (Eqs. (3)–(6)). Numbers in boxes are number of plots used for model parametrization. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
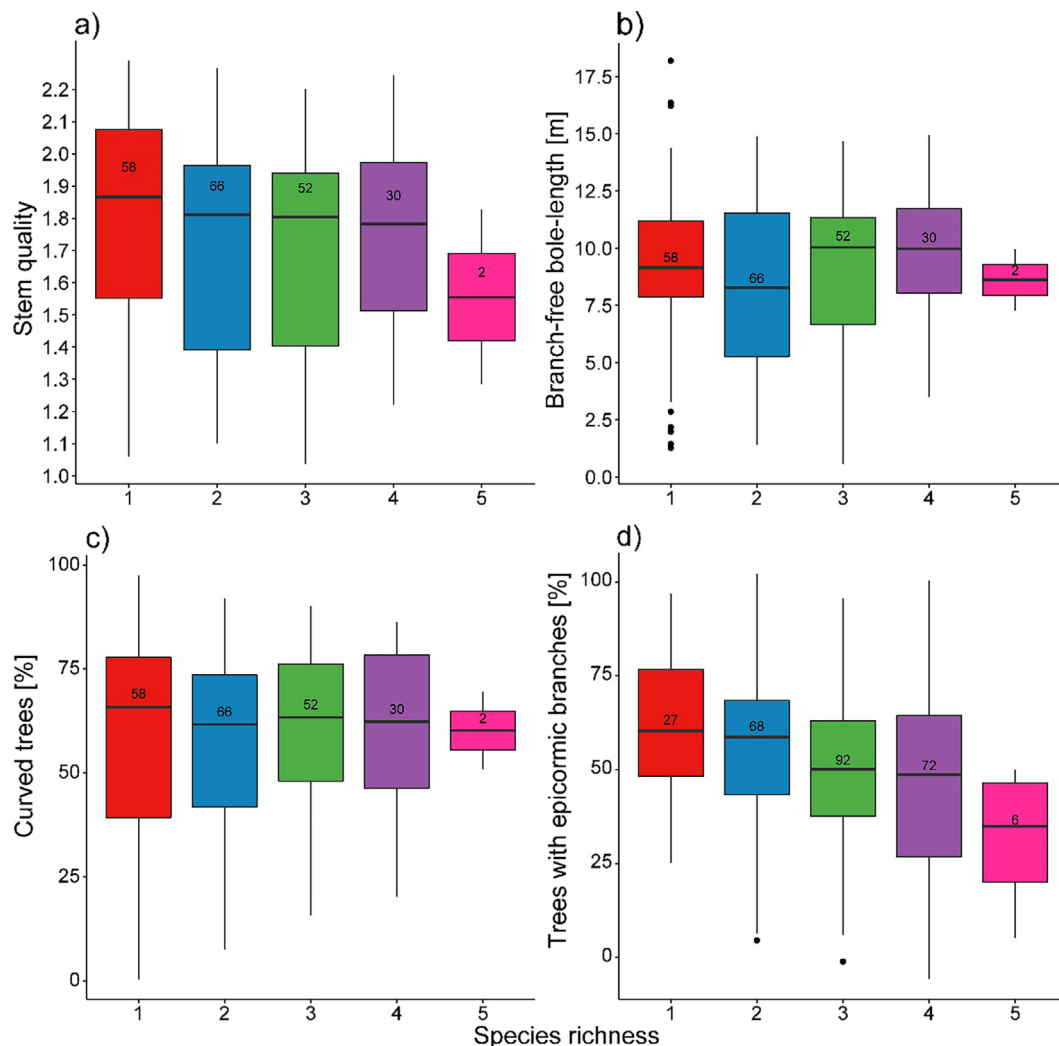
pattern regarding richness levels when considering individual species. The Mediterranean oaks, *Q. robur* and *C. sativa* all showed the highest prevalence of epicormics in monocultures, whereas for two of the most shade tolerant species (*A. alba, F. sylvatica*), epicormic branch occurrence increased with increasing species richness. A third group (*C. betulus, O. carpinifolia, A. pseudoplatanus, F. excelsior*) showed no consistent pattern (Fig. 6 c). However, higher occurrence of epicormic branches with higher richness levels when compared to monocultures was only significant for *Q. ilex* (richness levels 3, 4, all p < 0.043). Epicormic branch occurrence was also significantly higher in small-diameter trees than in large-diameter trees and this trend was consistent for the full model and all richness levels (Fig. 6a). The same trend was also found for all regions except for Romania, where it was reversed. At the tree species level, we found significant interactions with stem ratio (the ratio of the branch-free bole-length and the total tree height). A majority of species had fewer epicormic branches in stands with higher average stem ratio, although for some species (*C. sativa, C. betulus, F. excelsior* and *Q. cerris*), an increase in stem ratio was associated with a higher prevalence of epicormics (Table 3). In addition, most species were more susceptible to epicormic branching as the number of leaning stems in the plot increased, with only two exceptions showing the opposite trend (*F. excelsior* and *O. carpinifolia*). Lastly, the prevalence of epicormics within a stand was related to the level of competition within the plot, expressed as the per-plot sum of the

product of approximate tree volume (DBH^2 × height) and average wood density. Overall, epicormic branch occurrence decreased from about 55% in plots with lowest competition to about 45% in plots with highest competition. This trend held true for the regions Poland, Romania and Spain, while the opposite was found for Germany and Italy. Considering the effect of increasing species richness, we found that competition reduced the number of epicormics at low levels, but increased the occurrence of epicormic branches at high levels of species richness (Fig. 6b).

3.5. Mean stem quality and species identity

For 17 target species, the lack of a distinct significant negative relationship between tree species richness and average 'stem quality' per plot was confirmed when we used a model that took into account species identity (see Supporting Information S1-6). In essence, the model results show that there was no relationship between tree species richness and stem quality (Fig. 7).

4. Discussion

Our study set out to investigate whether tree species richness significantly reduces stem quality in a large number of European forest stands. There was no significant relationship between tree species

Table 2

Results from likelihood-ratio tests for the four models (Eqs. (3)–(6)) with P-values (based on Satterthwaite approximation implemented in the *lmerTest* package). The two bottom lines give marginal and conditional Pseudo-R^2 (goodness of fit) for each model, with marginal R^2 indicating the variance explained by fixed factors only and conditional R^2 the variance explained by fixed and random factors.

Predictors	Stem quality	Height to Crown Base	Curving	Epicormics
Tree species richness	0.232	0.235	0.657	0.130
DBH	0.000		0.006	0.000
Dominance class	0.043	0.000		
Crown roundness	0.003	0.038		
Crown roundness^2		0.024		
Lean			0.000	0.004
Latitude	0.004			
Stem ratio				0.043
Crown ratio	0.000			
Height-diameter-ratio		0.000		
Clade			0.000	
Species				0.000
Competition index (WD)				0.031
Competition index (ST) (square-root transformed)		0.000		
Lean × Clade			0.000	
Species × Stem ratio				0.005
Species × Lean				0.000
R^2 marginal	0.709	0.785	0.745	0.519
R^2 conditional	0.771	0.867	0.802	0.620

richness and mean 'stem quality' (or any of the stem quality variables measured) at the plot/stand-level, although there were slightly higher stem qualities in monocultures than in mixed stands. Our total model explained around 60 percent of the variation in stand-level quality-scores across European forests and tree species richness turned out to be the only non-significant predictor overall, for each of the species considered (Figs. 2 and 7).

However, in contrast to previous studies (e.g. Grotta et al., 2004; Kaitaniemi and Lintunen, 2010; Kuehne et al., 2013; Rock et al., 2004; Saha et al., 2014), the range of variables considered at the regional, community, and plot level enabled us to contribute to a comprehensive understanding of the most important factors behind the current stem quality distribution for a wide range of European forest types. Also, we found that neither site characteristics nor species composition at the community level strongly impacted plot-level stem quality. Instead, individual stand-level characteristics such as distribution of crown dominance levels and competition influenced stem quality the most. Owing to the fact that we measured tree quality only at one point in time, we could neither assess nor exclude the influence of past management and processes such as changes in stand density (through self-thinning or silvicultural thinning), damage from pests, pathogens or felling activities and self-pruning, which likely influenced stem quality.

4.1. Stem quality score

Stem quality is often described as an aggregate of the key factors straightness, branchiness, wood density and regularity of growth (tree ring width consistency and eccentricity) (Pretzsch and Rais, 2016; van Leeuwen et al., 2011). Many plot-level and single-tree-level factors influence these characteristics and our goal was to investigate the factors attributable to species diversity at the plot level. Pretzsch and Rais (2016) emphasised that structural complexity, which may increase with species diversity, is probably the most influential factor, rather than species diversity itself. They found a negative relationship between stem quality and species richness for many quality-relevant tree characteristics. In our study, the slopes of this relationship were also negative, but not significant. Results from our study do not definitively support their explanation that more species-diverse stands are

structurally more complex and that this generally influences stem quality negatively. Rather, our findings suggest that a potentially higher structural diversity may benefit some species' quality development while hindering that of other species. For example, some species showed a positive relationship (*F. excelsior*, *P. sylvestris*, *A. pseudoplatanus*, *Q. petraea* and *Q. ilex*, Fig. 7b), while others, especially *A. alba*, exhibited a negative association between quality and species richness (Fig. 7a + b). These contrasting patterns at the species level offset each other at the whole community level where the species richness effects were negligible and non-significant.

It is likely that species richness may be more sensibly interpreted as a proxy for structural diversity than as a primary factor. That is, structural heterogeneity leads to differences in light availability within a stand (Pretzsch and Rais, 2016) and light availability is potentially a major driver of how an individual trees crown architecture will develop (Dong et al., 2016; Medhurst et al., 2011; Pretzsch and Rais, 2016). Therefore, a mixed forest can be favourable or detrimental to stem quality and this will depend on the ecological traits of a species, namely its growth potential, its crown plasticity and its shade tolerance (Dong et al., 2016; Medhurst et al., 2011; Pretzsch and Rais, 2016). Exactly which species may profit from mixture with certain other species and which one may not, can only be rigorously investigated at the single-tree level taking into account its immediate tree neighbourhood. Silvicultural systems for mixtures have been designed accordingly. An example is a nurse system where a fast growing species is used to protect or shade a slower growing shade-tolerant species, so that the form of the latter is improved (Bauhus et al., 2017).

4.2. Branch-free bole-length

The most important factor for achieving high branch-free bole lengths is shading by surrounding trees. We found evidence that competition increased the branch-free bole length in the studied stands significantly and strongly, and this trend was consistent for all levels of species richness (Fig. 4a). The fact that there were no distinguishable differences between the richness levels leads us to conclude that there is little evidence for a distinct effect of tree species richness *per se* on the amount of branch-free stemwood. In accordance with the findings reported by Pretzsch and Rais (2016), there was also a linear relationship between 'branch-free bole-length' and slenderness (the ratio between height and diameter), which is a measure for the level of competition experienced by trees. While there was a large variation regarding the strength of the relationship, it did not vary significantly between the species richness levels (Fig. 4b). We interpret this as evidence that the most important factor determining branchiness and slenderness is indeed competition – and that it is of far greater importance than the difference between species participating in a mixture, at least at the plot level.

4.3. Stem curvature

For commercial wood production, stem curvature is among the most important defects (Richter, 2015). Despite this obvious importance for stem quality grading, no study that we know of has investigated the causes or prevalence of curvature systematically. In contrast, several studies have examined tree crown plasticity, which is the extent to which trees adapt the position and shape of their crowns under competitive pressure and to benefit from better light conditions (Brisson, 2001; Longuetaud et al., 2013; Schröter et al., 2012). None of these studies mention leaning stems or stem curvature as a result of this plastic crown reaction. Since the observed tree crowns with leaning stems or stem curvature in our study sites did not necessarily have asymmetric crowns, we hypothesised that 'curvature' in mixed stands could be a second mechanism to achieve crown plasticity, or an optimised exposure to the available light within irregular growing spaces. We found that 'curvature' occurred in all regions and for all species. We

Table 3

Parameter estimates for all four models (Eqs. (3)–(6)) and standard errors (parentheses). Asterisks indicate significance at confidence intervals of 95% ([*]), 99% ([**]) and 99.9% ([***]). Significance of levels of factorial predictors does not indicate overall significance of the factorial predictor. P-values for each predictor are given in Table 2.

	Quality	Stem length	Curvature	Epicormics
(Intercept)	−0.09 (0.42)	−41.85 (25.22)	0.65 (0.07)***	1.86 (0.35)***
richn_tar2	−0.07 (0.04)*	−0.49 (0.42)	0.02 (0.03)	−0.08 (0.06)
richn_tar3	−0.08 (0.04)*	−1.02 (0.44)*	−0.01 (0.03)	−0.13 (0.06)*
richn_tar4	−0.06 (0.05)	−0.75 (0.51)	0.02 (0.04)	−0.07 (0.06)
richn_tar5	−0.08 (0.13)	−0.44 (1.33)	−0.05 (0.09)	−0.27 (0.12)*
DBH	1.58 (0.26)***		−0.45 (0.16)**	
Dominance	−0.09 (0.04)*	−2.93 (0.38)***		
Crown roundness	1.20 (0.40)**	128.28 (60.94)*		
Crown ratio	−0.01 (0.00)***			
Latitude	0.03 (0.01)***			
sqrt(competition index (ST))		9.67 (0.82)***		
Crownroundness^2		−84.28 (36.86)*		
HD-Ratio		0.07 (0.01)***		
Lean			0.38 (0.08)***	
Conifer			−0.42 (0.06)***	
Mixed			−0.30 (0.06)***	
Lean × Conifer			0.47 (0.13)***	
Lean × Mixed			0.41 (0.11)***	
DBH				−0.82 (0.17)***
speciesAcer pseudoplatanus				−0.59 (0.38)
speciesCarpinus betulus				−1.82 (0.43)***
speciesCastanea sativa				−1.64 (0.44)***
speciesFagus sylvatica				−0.68 (0.37)
speciesFraxinus excelsior				−1.17 (0.47)*
speciesOstrya carpinifolia				−0.57 (0.78)
speciesQuercus cerris				−1.47 (0.42)***
speciesQuercus faginea				−1.08 (0.43)*
speciesQuercus ilex				−1.49 (0.39)***
speciesQuercus robur				−1.28 (0.38)***
Stemratio				−1.90 (0.67)**
Lean				0.09 (0.32)
Competition index (WD)				0.14 (0.06)*
speciesAcer pseudoplat. × stemratio				0.47 (0.76)
speciesCarpinus betulus × stemratio				2.79 (0.95)**
speciesCastanea sativa × stemratio				2.02 (0.82)*
speciesFagus sylvatica × stemratio				0.82 (0.76)
speciesFraxinus excelsior × stemratio				2.11 (0.89)*
speciesOstrya carpinifolia × stemratio				1.72 (0.91)
speciesQuercus cerris × stemratio				2.58 (0.89)**
speciesQuercus faginea × stemratio				0.87 (0.99)
speciesQuercus ilex × stemratio				1.78 (0.86)*
speciesQuercus robur × stemratio				1.61 (0.81)*
speciesAcer pseudoplatanus × lean				0.31 (0.34)
speciesCarpinus betulus × lean				0.89 (0.47)
speciesCastanea sativa × lean				0.81 (0.41)
speciesFagus sylvatica × lean				−0.02 (0.36)
speciesFraxinus excelsior × lean				−0.83 (0.38)*
speciesOstrya carpinifolia × lean				−0.67 (0.81)
speciesQuercus cerris × lean				−0.05 (0.38)
speciesQuercus faginea × lean				0.88 (0.38)*
speciesQuercus ilex × lean				0.56 (0.35)
speciesQuercus robur × lean				0.15 (0.37)
AIC	−41.70	834.74	−219.41	33.29
BIC	1.69	878.13	−172.68	180.06
Log Likelihood	33.85	−404.37	123.70	24.36
Num. obs.	208	208	208	265
Num. groups: composition	95	95	95	84
Num. groups: region	6	6	6	
Variance: composition. (Intercept)	0.00	0.93	0.00	0.01
Variance: region. (Intercept)	0.01	0.48	0.00	
Variance: Residual	0.03	2.28	0.01	0.04

could, however, not detect a clear influence of species richness on the prevalence of curvature within our study plots. Since 'stem curvature' might be a species-specific adaption to improve light availability, this stand-level analysis may represent the mean of contrasting species level responses, as was the case for stem quality scores.

Among the factors influencing the proportion of curved stems, the most important were tree size and the proportion of leaning stems. On

the one hand, this meant that 'curvature' either was less prevalent in larger trees than in smaller ones or that 'curvature' was either 'out-grown' to a degree with tree age, or that trees with curved stems had been preferentially removed through thinning in the past (Fig. 5a). On the other hand, stands with more leaning trees also exhibited more curved stems, but again, there were no significant differences between any of the species richness levels (Fig. 5b). Based on the assumption
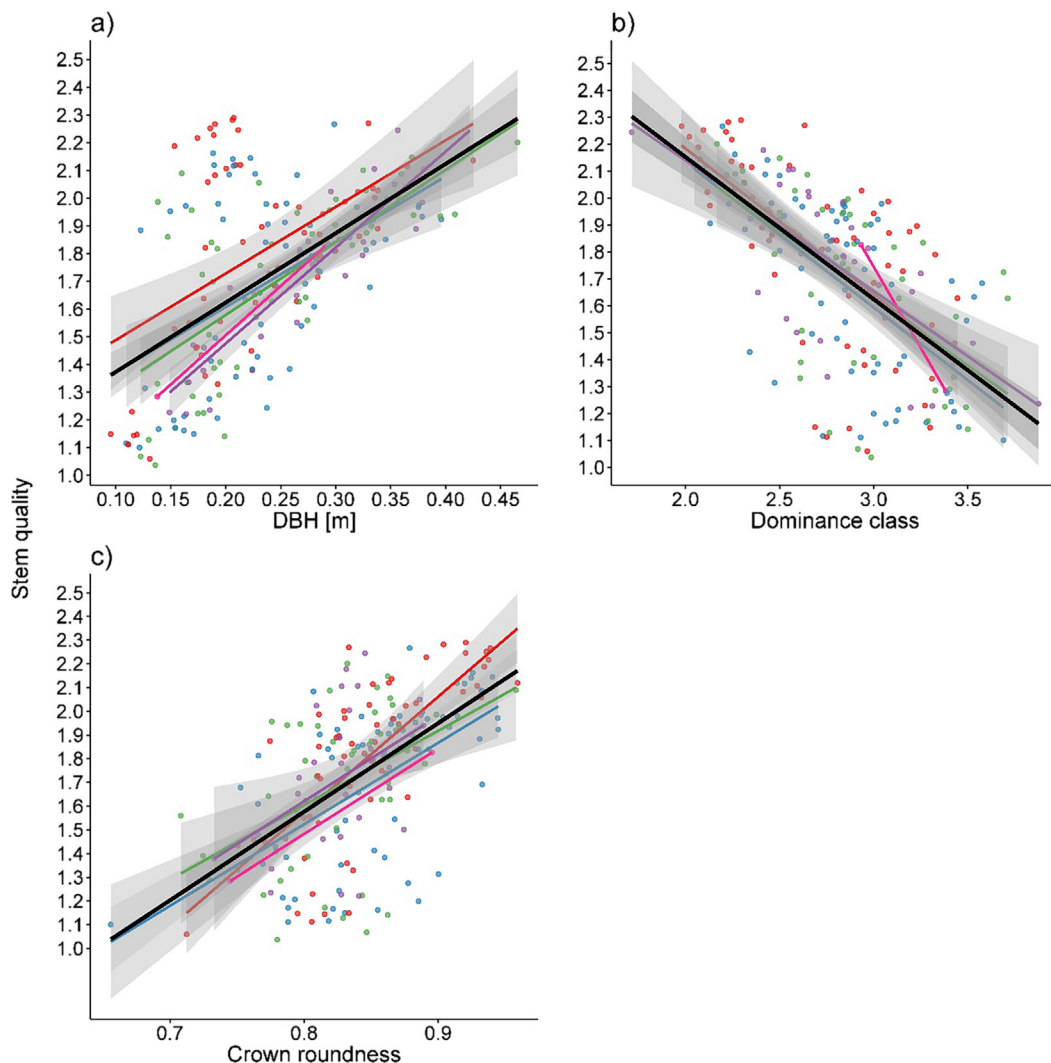
Fig. 3. Effects of DBH (a), crown dominance class (b) and crown roundness (c) on plot mean stem quality. Individual regression lines are shown for tree species richness levels (1 = red, 2 = blue, 3 = green, 4 = purple, 5 = pink) and the overall regression line (black). Shaded regions show the 95% confidence interval range. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

that conifers exhibit less curvature in general, we separated the data into the groups broadleaved, conifers and broadleaved-conifer-mixtures to detect differences regarding the relationship between leaning and curvature. However, we found that the relationship was robust, regardless of these groups and regardless of the level of species richness. This suggests that there is no higher risk of curved stems in mixtures or that stem lean and curvature might be controllable at the single-tree level, for example by guaranteeing that species with strong phototropic
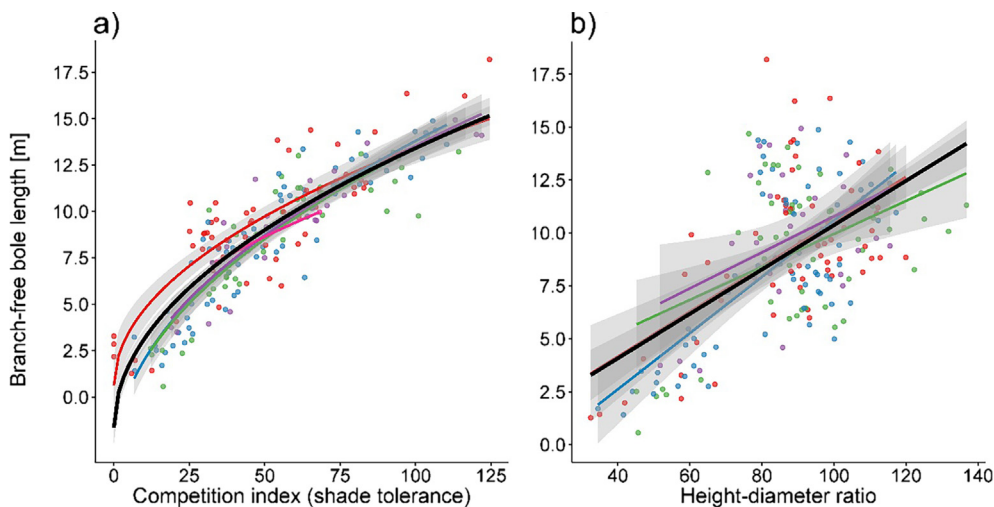
Fig. 4. Effects of competition (a) and height-diameter-ratio (b) on branch-free bole-length. Individual regression lines are shown for tree species richness levels (1 = red, 2 = blue, 3 = green, 4 = purple, 5 = pink) and the overall regression line from the mixed-effect model (black). Competition index was square-root transformed. Shaded regions show the 95% confidence interval range. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
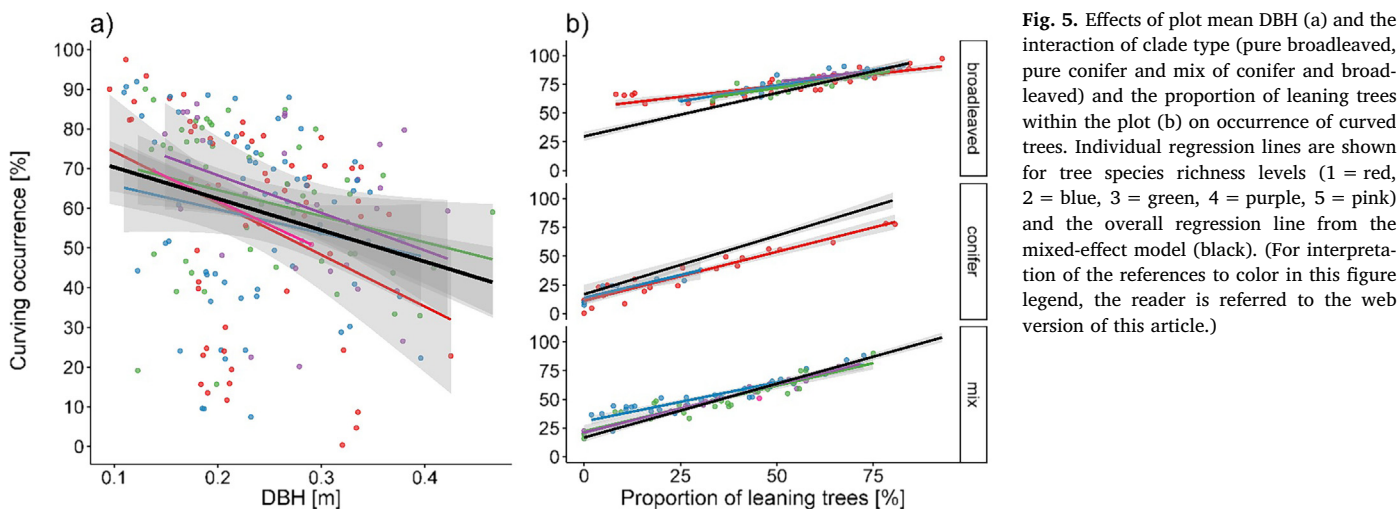
Fig. 5. Effects of plot mean DBH (a) and the interaction of clade type (pure broadleaved, pure conifer and mix of conifer and broadleaved) and the proportion of leaning trees within the plot (b) on occurrence of curved trees. Individual regression lines are shown for tree species richness levels (1 = red, 2 = blue, 3 = green, 4 = purple, 5 = pink) and the overall regression line from the mixed-effect model (black). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
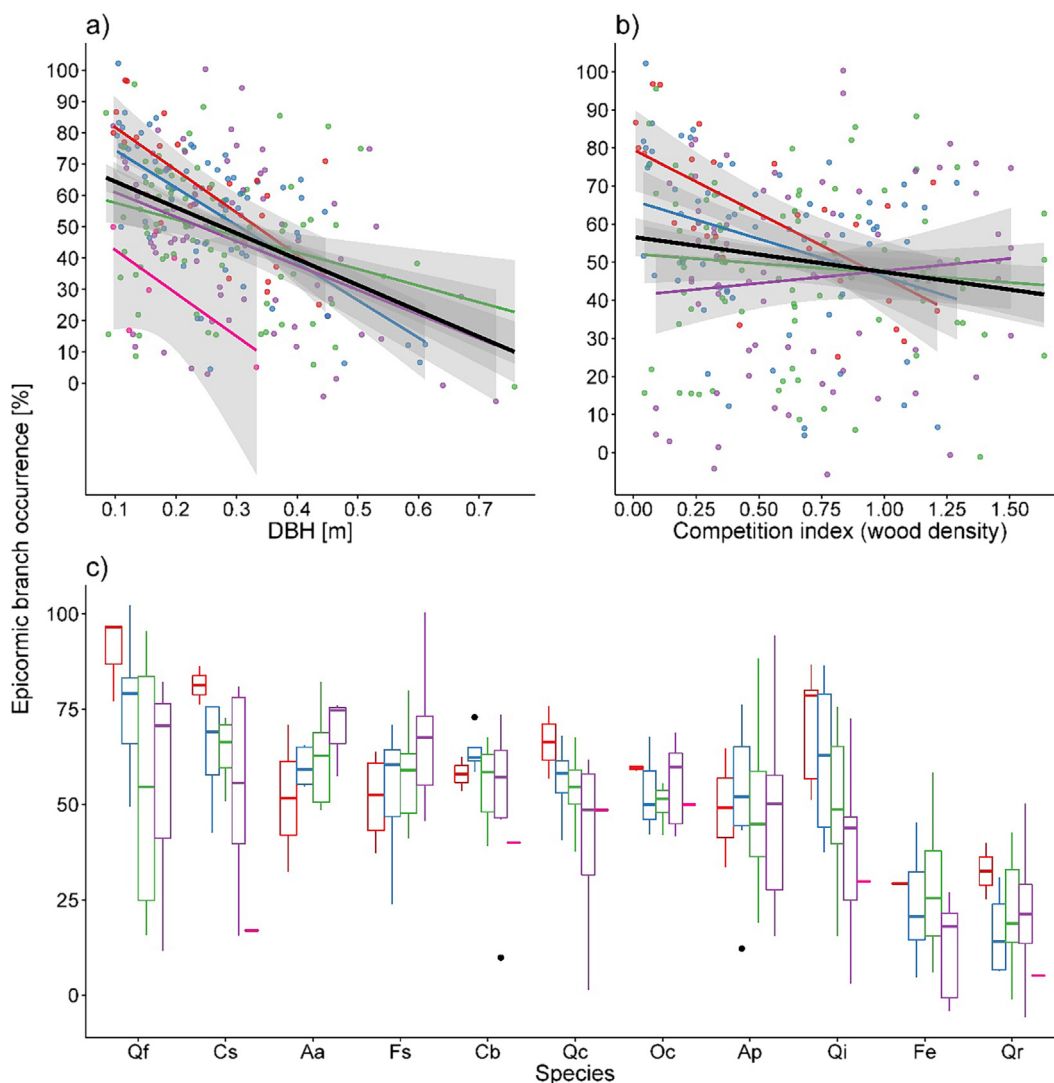
Fig. 6. Effects of plot mean DBH (a) competition (b) and species identity (c) on the occurrence of trees with epicormic branches. Individual regression lines are shown for tree species richness levels (1 = red, 2 = blue, 3 = green, 4 = purple, 5 = pink) and the overall regression line from the mixed-effect model (black). Boxplots show epicormic branch occurrence by species and richness levels per species, ordered by median per species (c). Species abbreviations can be found in Supporting Information S1-3, Table S3-2. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
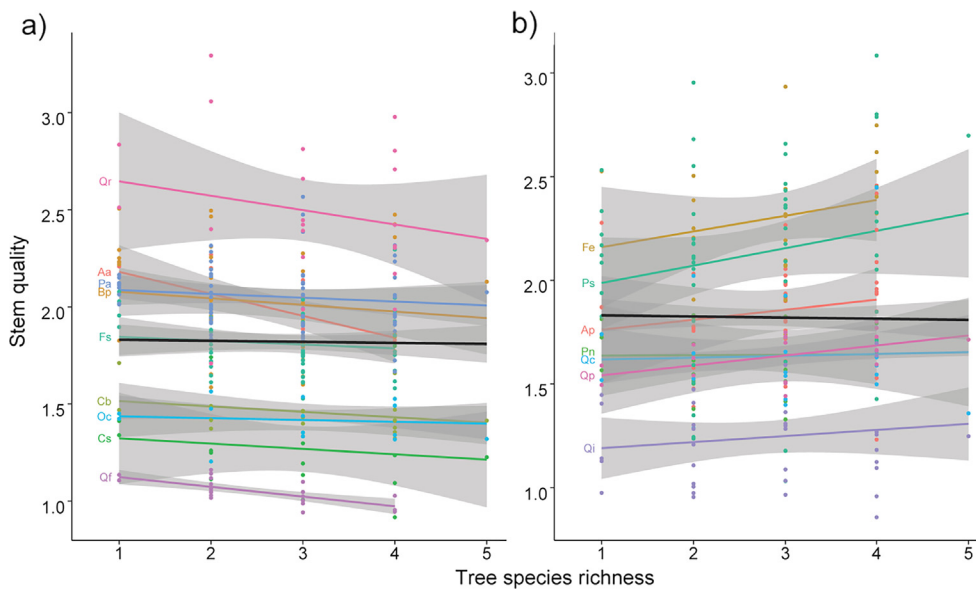
Fig. 7. Effects of tree species richness on plot mean stem quality for 17 tree species (see Supporting Information S1-3 for a full target species list). Individual regression lines are shown for each species, separately for negative slopes (a) and positive slopes (b) with overall regression line from the mixed-effect model (black). Species codes next to the regression lines consist of one letter for the genus and one letter for the species (e.g. Abies alba = Aa).

growth are given special attention regarding the maintenance of regular and sufficient growing space over time, regardless of whether they occur in mixtures or of the type of these mixtures. Notably, the proportion of curved stems was highest in Spain and in Italy (Supporting Information 1), where many forests were regenerated predominately from coppice. The origin of multiple stems from the same stump is known to increase the incidence of stem curvature (e.g. Bailey and Harjanto, 2005), unless the number of stump sprouts is reduced through management early in the production cycle (e.g. Everard and Christie, 1995).

4.4. Epicormic branches

With branchiness being probably the single most influential determinant of stem and wood quality (e.g. Montagu et al., 2003), many tree species may show quality detriment by forming secondary branches after the desired 'branch-free bole-length' has been achieved. Epicormic branches have the potential to devalue an otherwise high-quality stem section.

Epicormic branches may form as a result of stress (e.g. intense shading), defoliation in the crown, or suddenly increased light availability (Blum, 1963; Meadows and Burkhardt, 2001). In our study, we were interested in determining whether mixed-species stands generally produce more epicormic branches. There was no general hypothesis at the outset regarding this, as mixed stands may provide a greater variability in light conditions potentially increasing the risk for epicormic branch growth. Conversely, trees in mixed stands may be at lower risk of defoliation through specialist herbivorous insects (Jactel et al., 2017) and mixed stands may be more stratified than less diverse stands which could lead to inhibited epicormic growth due to more intense shading of lower tree trunks.

Our results showed that generally, smaller-diameter trees exhibited more epicormic branches (Fig. 6a). This may be explained by the concept of traumatic iteration due to suppression and severe competition. These stressed trees do not produce sufficient amounts of the hormone auxin, which suppresses the development of epicormic shoots from dormant buds (Meier et al., 2012). Notably, this trend was the same for all levels of diversity. However, fewer epicormic branches were found in stands with higher species richness and most trees with epicormic branches were actually present in pure stands. Since we removed those species not capable of developing epicormic branches from this particular analysis, it seems unlikely that this is an effect of dilution of species that can develop epicormics in the pool of epicormic-

free species. In such a large dataset with small effect sizes attained in the other models, even for significant relationships, this small effect would not have been registered by the model. In addition, many of the species considered here occurred mainly with other species also capable of producing epicormics and showed highest occurrences in the pure stands, such as, *Q. cerris, Q. faginea, Q. ilex, Q. robur*, and *C. sativa* (Fig. 6c). Moreover, there were also species showing the opposite trend, most notably *A. alba* and *F. sylvatica*. Since they occurred together and also with species not able to produce epicormics, they should have shown the reverse trend in the case of dilution. For the same forest plots across Europe, Jucker et al. (2015) showed that stratification in mixed stands is higher and canopy packing is more intense. This could also suppress the formation of epicormic branches, because less light reaches the lower stem sections, similar to the effects of "trainer" species. Another explanation could be that interspecific competition in pure stands is more severe and leads suppressed individuals to form epicormics to a greater degree than is the case in stands characterised by higher intra-specific competition (Fig. 6b). Our finding that increased competition in pure stands led to a reduction in epicormic branching, but only to the level of that in mixed stands where competition seemed to have almost no effect, may support this conclusion. These results further support knowledge about "trainer" effects in mixed stands and also provide evidence that mixed stands may actually help in controlling stem devaluation by epicormic branches (Bauhus et al., 2017).

4.5. Conclusions

Our results indicate that high-quality stems can be produced in species-rich forests, even if tree species richness did not influence timber quality *per se* in the studied European forests. Focusing on maintaining certain properties of stands (stratification) and single trees (enough growing space for forming round crowns, competition management for promoting branch shedding or pruning) is likely to be an efficient silvicultural approach for producing high-quality timber, regardless of compositional diversity of forest stands. Currently, the "future crop-tree management approach" seems to be a suitable option, as it focusses on optimizing single-tree development through maintaining round crowns and continuous growth. In our data, monocultures exhibited slightly better quality for most species, albeit none of these relations was significant. But even if a detailed single-tree level analysis would produce evidence that interspecific interactions would be detrimental to stem quality for some species, group-wise mixing of species

could be a solution to combine the higher structural uniformity of pure stands with potentially higher ecological stability and ecosystem service provision of compositionally diverse stands that has been shown for the same European forests (van der Plas et al., 2016). The complexity in terms of age and vertical structure within such stands may also provide more flexibility when faced with challenges such as rapidly fluctuating timber market demands and climate change. Diversity can by definition not produce uniformity – but growing conditions of individual trees, even in highly diverse mixtures, can be silviculturally managed to minimise adverse influences of compositional and structural diversity on timber quality.

Acknowledgements

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.2018.04.030.

References

Akaike, H., 1974. A new look at the statistical model identification. Autom. Control IEEE Trans. 19, 716–723. http://dx.doi.org/10.1109/TAC.1974.1100705.

Auguie, B., 2016. gridExtra: Miscellaneous Functions for "Grid" Graphics < http://CRAN.R-project.org/package=gridExtra > .

Baeten, L., Verheyen, K., Wirth, C., Bruelheide, H., Bussotti, F., Finér, L., Jaroszewicz, B., Selvi, F., Valladares, F., Allan, E., Ampoorter, E., Auge, H., Avăcăriei, D., Barbaro, L., Bărnoaiea, I., Bastias, C.C., Bauhus, J., Beinhoff, C., Benavides, R., Benneter, A., Berger, S., Berthold, F., Boberg, J., Bonal, D., Brüggemann, W., Carnol, M., Castagneyrol, B., Charbonnier, Y., Chećko, E., Coomes, D., Coppi, A., Dalmaris, E., Dănilă, G., Dawud, S.M., de Vries, W., De Wandeler, H., Deconchat, M., Domisch, T., Duduman, G., Fischer, M., Fotelli, M., Gessler, A., Gimeno, T.E., Granier, A., Grossiord, C., Guyot, V., Hantsch, L., Hättenschwiler, S., Hector, A., Hermy, M., Holland, V., Jactel, H., Joly, F.-X., Jucker, T., Kolb, S., Koricheva, J., Lexer, M.J., Liebergesell, M., Milligan, H., Müller, S., Muys, B., Nguyen, D., Nichiforel, L., Pollastrini, M., Proulx, R., Rabasa, S., Radoglou, K., Ratcliffe, S., Raulund-Rasmussen, K., Seiferling, I., Stenlid, J., Vesterdal, L., von Wilpert, K., Zavala, M.A., Zielinski, D., Scherer-Lorenzen, M., 2013. A novel comparative research platform designed to determine the functional significance of tree species diversity in European forests. Perspect. Plant Ecol. Evol. Syst. 15, 281–291. http://dx.doi.org/10.1016/j.ppees.2013.07.002.

Bailey, J.D., Harjanto, N.A., 2005. Teak (*Tectona grandis* L.) tree growth, stem quality and health in coppiced plantations in Java, Indonesia. New For. 30, 55–65. http://dx.doi.org/10.1007/s11056-004-1116-5.

Barton, K., 2015. MuMIn: Multi-Model Inference < http://CRAN.R-project.org/package=MuMIn > .

Bates, D., Mächler, M., Bolker, B., Walker, S., 2014. Fitting linear mixed-effects models using lme4. ArXiv E-Prints. http://dx.doi.org/10.18637/jss.v067.i01.

Bauhus, J., Forrester, D.I., Pretzsch, H., Felton, A., Pyttel, P., Benneter, A., 2017. Silvicultural options for mixed-species stands. In: Pretzsch, H., Forrester, D.I., Bauhus, J. (Eds.), Mixed-Species Forests: Ecology and Management. Springer, Berlin, Heidelberg, pp. 433–501. https://doi.org/10.1007/978-3-662-54553-9_9.

Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. For. Ecol. Manag. 258, 525–537. http://dx.doi.org/10.1016/j.foreco.2009.01.053.

Blum, B.M., 1963. Excessive exposure stimulates epicormic branching in young northern hardwoods. USDA For. Serv. Res. Note 1–6.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.-S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol. Evol. 24, 127–135. http://dx.doi.org/10.1016/j.tree.2008.10.008.

Books, D.J., Tubbs, C.H., 1970. Relation of light to epicormic branching in sugar maple. USDA For. Serv. Reseach Note 93, 1–2.

Brisson, J., 2001. Neighborhood competition and crown asymmetry in *Acer saccharum*. Can J Res 31, 2151–2159. http://dx.doi.org/10.1139/x01-161.

Burschel, P., Huss, J., 1997. Grundriß des Waldbaus. Pareys Studientexte, Parey, Berlin.

Cardinale, B.J., Matulich, K.L., Hooper, D.U., Byrnes, J.E., Duffy, E., Gamfeldt, L., Balvanera, P., O'Connor, M.I., Gonzalez, A., 2011. The functional role of producer diversity in ecosystems. Am. J. Bot. 98, 572–592. http://dx.doi.org/10.3732/ajb.1000364.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. Ecol. Lett. 12, 351–366. http://dx.doi.org/10.1111/j.1461-0248.2009.01285.x.

Dănescu, A., Ehring, A., Bauhus, J., Albrecht, A., Hein, S., 2015. Modelling discoloration and duration of branch occlusion following green pruning in *Acer pseudoplatanus* and *Fraxinus excelsior*. For. Ecol. Manag. 335, 87–98. http://dx.doi.org/10.1016/j.foreco.2014.09.027.

Dong, T.L., Forrester, D.I., Beadle, C., Doyle, R., Hoang, N.H., Giap, N.X., Worledge, D., 2016. Effects of light availability on crown structure, biomass production, light absorption and light-use efficiency of *Hopea odorata* planted within gaps in *Acacia* hybrid plantations. Plant Ecol. Divers. 9, 535–548. http://dx.doi.org/10.1080/17550874.2016.1262471.

Dowle, M., Short, T., Lianoglou, S., Saporta, A.S. with contributions from R., Antonyan, E., 2014. data.table: Extension of data.frame. < http://CRAN.R-project.org/package=data.table >

Erickson, H.D., Harrison, A.T., 1974. Douglas-fir wood quality studies part I: effects of age and stimulated growth on wood density and anatomy. Wood Sci. Technol. 8, 207–226. http://dx.doi.org/10.1007/BF00352024.

European Commission, 2008a. EN 1927-1:2008: Classification of softwood round timber – Part 1: Spruces and firs; German version.

European Commission, 2008b. EN 1927-2:2008: Qualitative classification of softwood round timber – Part 2: Pines; German version.

European Commission, 1997. EN 1316-1:1997: Hardwood round timber – Qualitative classification – Part 1: Oak and beech; German version.

Everard, J., Christie, J.M., 1995. Sweet chestnut: silviculture, timber quality and yield in the Forest of Dean. For. Int. J. For. Res. 68, 133–144. http://dx.doi.org/10.1093/forestry/68.2.133.

Forrester, D.I., Bauhus, J., 2016. A review of processes behind diversity—productivity relationships in forests. Curr. For. Rep. 2, 45–61. http://dx.doi.org/10.1007/s40725-016-0031-2.

Forrester, D.I., Benneter, A., Bouriaud, O., Bauhus, J., 2017. Diversity and competition influence tree allometric relationships – developing functions for mixed-species forests. J. Ecol. 105, 761–774. http://dx.doi.org/10.1111/1365-2745.12704.

Forrester, D.I., Collopy, J.J., Beadle, C.L., Baker, T.G., 2012. Interactive effects of simultaneously applied thinning, pruning and fertiliser application treatments on growth, biomass production and crown architecture in a young *Eucalyptus nitens* plantation. For. Ecol. Manage. 267, 104–116. http://dx.doi.org/10.1016/j.foreco.2011.11.039.

Fox, J., Weisberg, S., 2011. An R Companion to Applied Regression, second. ed. Sage, Thousand Oaks CA.

Gamfeldt, L., Snall, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C., Froberg, M., Stendahl, J., Philipson, C.D., Mikusinski, G., Andersson, E., Westerlund, B., Andren, H., Moberg, F., Moen, J., Bengtsson, J., 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. Nat. Commun. 4, 1340. http://dx.doi.org/10.1038/ncomms2328.

Grotta, A.T., Gartner, B.L., Radosevich, S.R., 2004. Influence of species proportion and timing of establishment on stem quality in mixed Red alder-Douglas-fir plantations. Can. J. For. Res. 34, 863–873. http://dx.doi.org/10.1139/x03-259.

Hajek, P., Seidel, D., Leuschner, C., 2015. Mechanical abrasion, and not competition for light, is the dominant canopy interaction in a temperate mixed forest. For. Ecol. Manage. 348, 108–116. http://dx.doi.org/10.1016/j.foreco.2015.03.019.

Hein, S., 2009. Modeling natural pruning of common ash, sycamore and wild cherry. In: Spiecker, H., Makkonen-Spiecker, M., Thies, M. (Eds.), Valuable Broadleaved Forests in Europe. Brill Academic Publishers, pp. 103–122.

Hocking, T.D., 2013. Directlabels: Direct labels for multicolor plots in lattice or ggplot2 < http://CRAN.R-project.org/package=directlabels > .

Jactel, H., Bauhus, J., Boberg, J., Bonal, D., Castagneyrol, B., Gardiner, B., Gonzalez-Olabarria, J.R., Koricheva, J., Meurisse, N., Brockerhoff, E.G., 2017. Tree diversity drives forest stand resistance to natural disturbances. Curr. For. Rep. 3, 223–243. http://dx.doi.org/10.1007/s40725-017-0064-1.

Jucker, T., Bouriaud, O., Coomes, D.A., 2015. Crown plasticity enables trees to optimize canopy packing in mixed-species forests. Funct. Ecol. 1078–1086. http://dx.doi.org/10.1111/1365-2435.12428.

Kaitaniemi, P., Lintunen, A., 2010. Neighbor identity and competition influence tree growth in Scots pine, Siberian larch, and silver birch. Ann. For. Sci. 67, 604. http://dx.doi.org/10.1051/forest/2010017.

Kelty, M.J., 2006. The role of species mixtures in plantation forestry. For. Ecol. Manage. 233, 195–204. http://dx.doi.org/10.1016/j.foreco.2006.05.011.

Kint, V., Hein, S., Campioli, M., Muys, B., 2010. Modelling self-pruning and branch attributes for young *Quercus robur* L. and *Fagus sylvatica* L. trees. For. Ecol. Manage. 260, 2023–2034. http://dx.doi.org/10.1016/j.foreco.2010.09.008.

Knoke, T., 2008. Mixed forests and finance – methodological approaches. Ecol. Econ. 65, 590–601. http://dx.doi.org/10.1016/j.ecolecon.2007.08.009.

Knoke, T., Stang, S., Remler, N., Seifert, T., 2006. Ranking the importance of quality variables for the price of high quality beech timber (*Fagus sylvatica* L.). Ann Sci 63, 399–413. http://dx.doi.org/10.1051/forest:2006020.

Kraft, G., 1884. Beiträge zur Lehre von den Durchforstungen. Schlagstellungen und Lichtungshieben. Klindworth's Verlag, Hannover.

Kramer, H., 1988. Waldwachstumslehre. Parey, Hamburg u.a.

Kuehne, C., Kublin, E., Pyttel, P., Bauhus, J., 2013. Growth and form of *Quercus robur* and *Fraxinus excelsior* respond distinctly different to initial growing space: results from 24-year-old Nelder experiments. J. For. Res. 24, 1–14. http://dx.doi.org/10.1007/s11676-013-0320-6.

Kunstler, G., Falster, D., Coomes, D.A., Hui, F., Kooyman, R.M., Laughlin, D.C., Poorter, L., Vanderwel, M., Vieilledent, G., Wright, S.J., Aiba, M., Baraloto, C., Caspersen, J., Cornelissen, J.H.C., Gourlet-Fleury, S., Hanewinkel, M., Herault, B., Kattge, J.,

Kurokawa, H., Onoda, Y., Peñuelas, J., Poorter, H., Uriarte, M., Richardson, S., Ruiz-Benito, P., Sun, I.-F., Ståhl, G., Swenson, N.G., Thompson, J., Westerlund, B., Wirth, C., Zavala, M.A., Zeng, H., Zimmerman, J.K., Zimmermann, N.E., Westoby, M., 2016. Plant functional traits have globally consistent effects on competition. Nature 529, 204–207. http://dx.doi.org/10.1038/nature16476.

Kuuluvainen, T., 2009. Forest management and biodiversity conservation based on natural ecosystem dynamics in Northern Europe: the complexity challenge. AMBIO J. Hum. Environ. 38, 309–315. http://dx.doi.org/10.1579/08-A-490.1.

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2014. lmerTest: Tests in linear mixed effects models < http://CRAN.R-project.org/package=lmerTest > .

Lang, A.C., Härdtle, W., Bruelheide, H., Geißler, C., Nadrowski, K., Schuldt, A., Yu, M., von Oheimb, G., 2010. Tree morphology responds to neighbourhood competition and slope in species-rich forests of subtropical China. For. Ecol. Manag. 260, 1708–1715. http://dx.doi.org/10.1016/j.foreco.2010.08.015.

Larson, P.R., 1963. Stem form development of forest trees. For. Sci. 9.

Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E.-D., McGuire, A.D., Bozzato, F., Pretzsch, H., de-Miguel, S., Paquette, A., Hérault, B., Scherer-Lorenzen, M., Barrett, C.B., Glick, H.B., Hengeveld, G.M., Nabuurs, G.-J., Pfautsch, S., Viana, H., Vibrans, A.C., Ammer, C., Schall, P., Verbyla, D., Tchebakova, N., Fischer, M., Watson, J.V., Chen, H.Y.H., Lei, X., Schelhaas, M.-J., Lu, H., Gianelle, D., Parfenova, E.I., Salas, C., Lee, E., Lee, B., Kim, H.S., Bruelheide, H., Coomes, D.A., Piotto, D., Sunderland, T., Schmid, B., Gourlet-Fleury, S., Sonké, B., Tavani, R., Zhu, J., Brandl, S., Vayreda, J., Kitahara, F., Searle, E.B., Neldner, V.J., Ngugi, M.R., Baraloto, C., Frizzera, L., Bałazy, R., Oleksyn, J., Zawiła-Niedźwiecki, T., Bouriaud, O., Bussotti, F., Finér, L., Jaroszewicz, B., Jucker, T., Valladares, F., Jagodzinski, A.M., Peri, P.L., Gonmadje, C., Marthy, W., O'Brien, T., Martin, E.H., Marshall, A.R., Rovero, F., Bitariho, R., Niklaus, P.A., Alvarez-Loayza, P., Chamuya, N., Valencia, R., Mortier, F., Wortel, V., Engone-Obiang, N.L., Ferreira, L.V., Odeke, D.E., Vasquez, R.M., Lewis, S.L., Reich, P.B., 2016. Positive biodiversity-productivity relationship predominant in global forests. Science 354. http://dx.doi.org/10.1126/science.aaf8957.

Longuetaud, F., Piboule, A., Wernsdörfer, H., Collet, C., 2013. Crown plasticity reduces inter-tree competition in a mixed broadleaved forest. Eur. J. For. Res. 132, 621–634. http://dx.doi.org/10.1007/s10342-013-0699-9.

Lüdecke, D., 2015. sjPlot: Data Visualization for Statistics in Social Science < http://CRAN.R-project.org/package=sjPlot > .

Mahler, G., Willmann, U., Wurster, M., 2001. Arbeitsanweisung für die Güteansprache am stehenden Stamm im Rahmen der 2. Bundeswaldinventur (BWI 2) in Baden-Württemberg - Operating Manual for Quality Grading of Standing Stems for the 2nd National Forest Inventory (BWI 2) < http://www.fva-bw.de/forschung/wn/bwi_gueteanspr/arbeitsanweisung.pdf > (accessed 1.14.15).

Mäkinen, H., 1999. Growth, suppression, death, and self-pruning of branches of Scots pine in southern and central Finland. Can. J. For. Res. 29, 585–594. http://dx.doi.org/10.1139/x99-026.

Meadows, J.S., Burkhardt, E.C., 2001. Epicormic branches affect lumber grade and value in willow oak. South. J. Appl. For. 25, 136–141.

Medhurst, J., Ottenschlaeger, M., Wood, M., Harwood, C., Beadle, C., Valencia, J.C., 2011. Stem eccentricity, crown dry mass distribution, and longitudinal growth strain of plantation-grown *Eucalyptus nitens* after thinning. Can. J. For. Res. 41, 2209–2218. http://dx.doi.org/10.1139/x11-135.

Medhurst, J.L., Pinkard, E.A., Beadle, C.L., Worledge, D., 2003. Growth and stem form responses of plantation-grown *Acacia melanoxylon* (R. Br.) to form pruning and nurse-crop thinning. For. Ecol. Manage. 179, 183–193. http://dx.doi.org/10.1016/S0378-1127(02)00521-2.

Meier, A.R., Saunders, M.R., Michler, C.H., 2012. Epicormic buds in trees: a review of bud establishment, development and dormancy release. Tree Physiol. 32, 565–584. http://dx.doi.org/10.1093/treephys/tps040.

Montagu, K.D., Kearney, D.E., Smith, R.G.B., 2003. The biology and silviculture of pruning planted eucalypts for clear wood production—a review. For. Ecol. Manage. 179, 1–13. http://dx.doi.org/10.1016/S0378-1127(02)00579-0.

Muradian, R., Arsel, M., Pellegrini, L., Adaman, F., Aguilar, B., Agarwal, B., Corbera, E., Ezzine de Blas, D., Farley, J., Froger, G., Garcia-Frapolli, E., Gómez-Baggethun, E., Gowdy, J., Kosoy, N., Le Coq, J.F., Leroy, P., May, P., Méral, P., Mibielli, P., Norgaard, R., Ozkaynak, B., Pascual, U., Pengue, W., Perez, M., Pesche, D., Pirard, R., Ramos-Martin, J., Rival, L., Saenz, F., Van Hecken, G., Vatn, A., Vira, B., Urama, K., 2013. Payments for ecosystem services and the fatal attraction of win-win solutions. Conserv. Lett. 6, 274–279. http://dx.doi.org/10.1111/j.1755-263X.2012.00309.x.

Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecol. Monogr. 76, 521–547. http://dx.doi.org/10.1890/0012-9615(2006) 076[0521:TTSDAW]2.0.CO;2.

Noss, R.F., 2001. Beyond Kyoto: forest management in a time of rapid climate change. Conserv. Biol. 15, 578–590. http://dx.doi.org/10.1046/j.1523-1739.2001.015003578.x.

Oliver, C.D., Larson, B.C., 1990. Forest Stand Dynamics. McGraw-Hill Inc, New York.

Ozanne, C.M.P., Anhuf, D., Boulter, S.L., Keller, M., Kitching, R.L., Körner, C., Meinzer, F.C., Mitchell, A.W., Nakashizuka, T., Dias, P.L.S., Stork, N.E., Wright, S.J., Yoshimura, M., 2003. Biodiversity meets the atmosphere: a global view of forest canopies. Science 301, 183–186. http://dx.doi.org/10.1126/science.1084507.

Paquette, A., Messier, C., 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. Glob. Ecol. Biogeogr. 20, 170–180. http://dx.doi.org/10.1111/j.1466-8238.2010.00592.x.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2015. nlme: Linear and Nonlinear Mixed Effects Models. < http://CRAN.R-project.org/package=nlme > .

Piotto, D., Craven, D., Montagnini, F., Alice, F., 2010. Silvicultural and economic aspects of pure and mixed native tree species plantations on degraded pasturelands in humid Costa Rica. New For. 39, 369–385. http://dx.doi.org/10.1007/s11056-009-9177-0.

Pretzsch, H., 2006. Species-specific allometric scaling under self-thinning: evidence from long-term plots in forest stands. Oecologia 146, 572–583. http://dx.doi.org/10.1007/s00442-005-0126-0.

Pretzsch, H., del Río, M., Ammer, C., Avdagic, A., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Dirnberger, G., Drössler, L., Fabrika, M., Forrester, D.I., Godvod, K., Heym, M., Hurt, V., Kurylyak, V., Löf, M., Lombardi, F., Matović, B., Mohren, F., Motta, R., den Ouden, J., Pach, M., Ponette, Q., Schütze, G., Schweig, J., Skrzyszewski, J., Sramek, V., Sterba, H., Stojanović, D., Svoboda, M., Vanhellemont, M., Verheyen, K., Wellhausen, K., Zlatanov, T., Bravo-Oviedo, A., 2015. Growth and yield of mixed versus pure stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) analysed along a productivity gradient through Europe. Eur. J. For. Res. 134, 927–947. http://dx.doi.org/10.1007/s10342-015-0900-4.

Pretzsch, H., Rais, A., 2016. Wood quality in complex forests versus even-aged monocultures: review and perspectives. Wood Sci. Technol. 50, 845–880. http://dx.doi.org/10.1007/s00226-016-0827-z.

Pretzsch, H., Schütze, G., 2009. Transgressive overyielding in mixed compared with pure stands of Norway spruce and European beech in Central Europe: evidence on stand level and explanation on individual tree level. Eur. J. For. Res. 128, 183–204. http://dx.doi.org/10.1007/s10342-008-0215-9.

Pukkala, T., 2002. Multi-objective forest planning., Managing Forest Ecosystems Volume 6. Kluwer Academic Publishers, Dordrecht.

Putz, F.E., Parker, G.G., Archibald, R.M., 1984. Mechanical abrasion and intercrown spacing. Am. Midl. Nat. 112, 24–28. http://dx.doi.org/10.2307/2425452.

Core Team, R., 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria http://CRAN.R-project.org.

Ratcliffe, S., Holzwarth, F., Nadrowski, K., Levick, S., Wirth, C., 2015. Tree neighbourhood matters – tree species composition drives diversity–productivity patterns in a near-natural beech forest. For. Ecol. Manage. 335, 225–234. http://dx.doi.org/10.1016/j.foreco.2014.09.032.

Richter, C., 2015. Wood Characteristics Inherent in a Tree's Natural Growth. In: Wood Characteristics: Description, Causes, Prevention, Impact on Use and Technological Adaptation. Springer International Publishing, Cham, pp. 35–124. https://doi.org/10.1007/978-3-319-07422-1_5.

Rock, J., Puettmann, K.J., Gockel, H.A., Schulte, A., 2004. Spatial aspects of the influence of silver birch (*Betula pendula* L.) on growth and quality of young oaks (*Quercus* spp.) in central Germany. Forestry 77, 235–247. http://dx.doi.org/10.1093/forestry/77.3.235.

Röhle, H., 1984. Ertragskundliche Merkmale von Stieleichen-Mischbeständen auf grundwasserbeeinflußten Standorten in den Auewaldgebieten Südbayerns – yield properties of Pedunculate oak mixed stands on groundwater-affected sites in Southern Bavarian riparian forests. Forstwiss. Cent. 103, 330–349.

Ruiz-Benito, P., Gómez-Aparicio, L., Paquette, A., Messier, C., Kattge, J., Zavala, M.A., 2014. Diversity increases carbon storage and tree productivity in Spanish forests. Glob. Ecol. Biogeogr. 23, 311–322. http://dx.doi.org/10.1111/geb.12126.

Ruiz-Jaen, M.C., Potvin, C., 2011. Can we predict carbon stocks in tropical ecosystems from tree diversity? Comparing species and functional diversity in a plantation and a natural forest. New Phytol. 189, 978–987. http://dx.doi.org/10.1111/j.1469-8137.2010.03501.x.

Saha, S., Kuehne, C., Bauhus, J., 2014. Intra- and interspecific competition differently influence growth and stem form of young oaks (*Quercus robur* L. and *Quercus petraea* (Mattuschka) Liebl.). Ann. For. Sci. 71, 381–393. http://dx.doi.org/10.1007/s13595-013-0345-1.

Sánchez-Gómez, D., Valladares, F., Zavala, M.A., 2006. Performance of seedlings of Mediterranean woody species under experimental gradients of irradiance and water availability: trade-offs and evidence for niche differentiation. New Phytol. 170, 795–806. http://dx.doi.org/10.1111/j.1469-8137.2006.01711.x.

Schröter, M., Härdtle, W., von Oheimb, G., 2012. Crown plasticity and neighborhood interactions of European beech (*Fagus sylvatica* L.) in an old-growth forest. Eur. J. For. Res. 131, 787–798. http://dx.doi.org/10.1007/s10342-011-0552-y.

Sterba, H., Vospernik, S., Söderbergh, I., Ledermann, T., 2006. Harvesting Rules and Modules for Predicting Commercial Timber Assortments. In: Hasenauer, H. (Ed.), Sustainable Forest Management. Springer, Berlin Heidelberg, pp. 111–129.

Takiya, M., Koyama, H., Umeki, K., Yasaka, M., Ohno, Y., Watanabe, I., Terazawa, K., 2010. The effects of early and intense pruning on light penetration, tree growth, and epicormic shoot dynamics in a young hybrid larch stand. J. For. Res. 15, 149–160. http://dx.doi.org/10.1007/s10310-009-0167-z.

Thies, M., Pfeifer, N., Winterhalder, D., Gorte, B.G.H., 2004. Three-dimensional reconstruction of stems for assessment of taper, sweep and lean based on laser scanning of standing trees. Scand. J. For. Res. 19, 571–581. http://dx.doi.org/10.1080/02827580410019562.

van der Plas, F., Manning, P., Allan, E., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., Zavala, M.A., Hector, A., Ampoorter, E., Baeten, L., Barbaro, L., Bauhus, J., Benavides, R., Benneter, A., Berthold, F., Bonal, D., Bouriaud, O., Bruelheide, H., Bussotti, F., Carnol, M., Castagneyrol, B., Charbonnier, Y., Coomes, D., Coppi, A., Bastias, C.C., Muhie Dawud, S., De Wandeler, H., Domisch, T., Finer, L., Gessler, A., Granier, A., Grossiord, C., Guyot, V., Hättenschwiler, S., Jactel, H., Jaroszewicz, B., Joly, F.-X., Jucker, T., Koricheva, J., Milligan, H., Muller, S., Muys, B., Nguyen, D., Pollastrini, M., Raulund-Rasmussen, K., Selvi, F., Stenlid, J., Valladares, F., Vesterdal, L., Zielinski, D., Fischer, M., 2016. Jack-of-all-trades effects drive biodiversity-ecosystem multifunctionality relationships in European forests. Nat. Commun. 7. http://dx.doi.org/10.1038/ncomms11109.

van Leeuwen, M., Hilker, T., Coops, N.C., Frazer, G., Wulder, M.A., Newnham, G.J., Culvenor, D.S., 2011. Assessment of standing wood and fiber quality using ground and airborne laser scanning: a review. For. Ecol. Manag. 261, 1467–1478. http://dx.doi.org/10.1016/j.foreco.2011.01.032.

Vilà, M., Carrillo-Gavilán, A., Vayreda, J., Bugmann, H., Fridman, J., Grodzki, W., Haase,

J., Kunstler, G., Schelhaas, M., Trasobares, A., 2013. Disentangling biodiversity and climatic determinants of wood production. PLoS ONE 8, e53530. http://dx.doi.org/10.1371/journal.pone.0053530.

von Lüpke, B., 1998. Silvicultural methods of oak regeneration with special respect to shade tolerant mixed species. For. Ecol. Manage. 106, 19–26. http://dx.doi.org/10.1016/S0378-1127(97)00235-1.

Wickham, H., 2009. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.

Wickham, H., 2007. Reshaping data with the reshape package. J. Stat. Softw. 21, 1–20.

Zobel, B., 1984. The changing quality of the world wood supply. Wood Sci. Technol. 18, 1–17. http://dx.doi.org/10.1007/BF00632127.