



Species proportions by area in mixtures of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.)

Gerald Dirnberger¹ · Hubert Sterba¹ · Sonia Condés² · Christian Ammer³ · Peter Annighöfer³ · Admir Avdagić⁴ · Kamil Bielak⁵ · Gediminas Brazaitis⁶ · Lluís Coll⁷ · Michael Heym⁸ · Václav Hurt⁹ · Viktor Kurylyak¹⁰ · Renzo Motta¹¹ · Maciej Pach¹² · Quentin Ponette¹³ · Ricardo Ruiz-Peinado¹⁴ · Jerzy Skrzyszewski¹² · Vít Šrámek¹⁵ · Géraud de Streel¹³ · Miroslav Svoboda¹⁶ · Tzvetan Zlatanov¹⁷ · Hans Pretzsch⁸

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Abstract Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) dominate many of the European forest stands. Also, mixtures of European beech and Scots pine more or less occur over all European countries, but have been scarcely investigated. The area occupied by each species is of high relevance, especially for growth evaluation and comparison of different species in mixed and monospecific stands. Thus, we studied different methods to describe species proportions and their definition as proportion by area. 25 triplets consisting of mixed and

monospecific stands were established across Europe ranging from Lithuania to Spain in northern to southern direction and from Bulgaria to Belgium in eastern to western direction. On stand level, the conclusive method for estimating the species proportion as a fraction of the stand area relates the observed density (tree number or basal area) to its potential. This stand-level estimation makes use of the potential from comparable neighboring monospecific stands or from maximum density lines derived from other data, e.g. forest inventories or permanent observations plots. At tree level, the fraction of the stand area occupied by a species can be derived from the

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✉ Gerald Dirnberger
gerald.dirnberger@boku.ac.at

¹ Department of Forest and Soil Sciences, Institute of Forest Growth, BOKU University of Natural Resources and Life Sciences, Peter-Jordan-Straße 82, 1190 Vienna, Austria

² Department of Natural Systems and Resources, School of Forestry, Technical University of Madrid, Madrid, Spain

³ Abteilung Waldbau und Waldökologie der gemäßigten Zonen, Georg-August-Universität Göttingen, Göttingen, Germany

⁴ Department for Forest Management and Urban Greenery, Faculty of Forestry, University Sarajevo, Sarajevo, Bosnia and Herzegovina

⁵ Department of Silviculture, Warsaw University of Life Sciences, Warsaw, Poland

⁶ Institute of Forest Biology and Silviculture, Aleksandras Stulginskis University, Kaunas, Lithuania

⁷ Department of Agriculture and Forest Engineering – Forest Sciences Centre of Catalonia (CTFC), University of Lleida, Lleida, Spain

⁸ Chair for Forest Growth and Yield Science, Technische Universität München, Munich, Germany

⁹ Department of Silviculture, Mendel University, Brno, Czech Republic

¹⁰ Forestry Academy of Sciences of Ukraine, Lviv, Ukraine

¹¹ Department of Agricultural, Forest and Food Sciences DISAFA, University of Turin, Turin, Italy

¹² Department of Silviculture, Institute of Forest Ecology and Silviculture, University of Agriculture, Krakow, Poland

¹³ Université Catholique de Louvain, Faculty of Bioscience Engineering & Earth and Life Institute, Louvain-la-Neuve, Belgium

¹⁴ Department of Silviculture and Forest Systems Management, INIA-CIFOR, Madrid, Spain

¹⁵ Forestry and Game Management Research Institute, Jíloviště, Czech Republic

¹⁶ Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Prague, Czech Republic

¹⁷ Department of Silviculture, Forest Research Institute, Sofia, Bulgaria

proportions of their crown projection area or of their leaf area. The estimates of the potentials obtained from neighboring monospecific stands, especially in older stands, were poorer than those from the maximum density line depending on the Martonne aridity index. Therefore, the stand-level method in combination with the Martonne aridity index for potential densities can be highly recommended. The species' proportions estimated with this method are best approximated by the proportions of the species' leaf areas. In forest practice, the most commonly applied method is an ocular estimation of the proportions by crown projection area. Even though the proportions of pine were calculated here by measuring crown projection areas in the field, we found this method to underestimate the proportion by 25% compared to the stand-level approach.

Keywords *Pinus sylvestris* · *Fagus sylvatica* · Species proportion by area · Mixture proportion · Potential density

Introduction

Since the middle of the last century, forest scientists and forest managers increasingly emphasized the importance of mixed forests. In the last decades, a number of studies have been published, which deal with the comparison of mixed stands and monospecific stands. These studies mainly investigated the effects of mixture on productivity (Kelty 1992; DeBell et al. 1997; Chen et al. 2003; Bristow et al. 2006; R o and Sterba 2009; Bielak et al. 2014; Cond es and R o 2015; Pretzsch et al. 2015; Pretzsch and Sch utze 2016), ecological functioning (Schmid and Kazda 2002; Schume et al. 2004; Pretzsch et al. 2016), natural hazards (Neuner et al. 2015; Metz et al. 2016), and economical risks (Knoke et al. 2008; Griess and Knoke 2011) or tried to evaluate the effect of several ecosystem services (Kelty 2006; Forrester and Pretzsch 2015; Felton et al. 2016). However, most studies neither dealt with adequate definitions of compositional proportions nor investigated possible effects of different definitions on the outcomes based on the assumed species proportions.

In mixed-species stands, species proportion is most frequently used to describe how species occupy growing space at the stand level. It is frequently applied in growth and yield studies, used for the interpretation of growth efficiency, and it is a common measure of stand descriptions in forest management practice (R o et al. 2016). Knowledge on the methods applied to estimate tree species proportions is of importance to better comprehend the results derived from studies dealing with differences in productivity between mixed and monospecific stands.

Most studies do not sufficiently discuss if the methods to derive mixture proportions are appropriate. Studies by

Dirnberger and Sterba (2014), Huber et al. (2014) and Sterba et al. (2014) showed that there could be considerable effects on species' productivity when comparing different approaches of estimating mixture proportions. Across all examples given by Dirnberger and Sterba (2014), the average under- or overyielding of spruce was estimated to range from -28 to $+25\%$, the respective values for beech ranged between -32 and $+21\%$, and the estimations of the total underyielding of the mixed stands ranged from -17 to -4% , in dependence of the chosen definition for species proportion. Especially if the expected growth differences between species in mixed stands are small, the importance of highly reliable estimations for mixture proportions becomes indispensable.

Depending on the study objectives, several methods for defining proportions have been suggested (Bravo-Oviedo et al. 2014). In their investigations, Dirnberger and Sterba (2014), Huber et al. (2014), and Sterba et al. (2014) already pointed out that proportions by area are needed to evaluate mixture effects. This is particularly true when comparing the productivity of mixed and monospecific stands, when growth has to be related to the area occupied by the different species, i.e. growth per hectare in the monospecific stand related to growth per hectare of the mixed stand. As a consequence, the species proportions have to represent the species-specific fraction of the stand area, i.e. the area on which the species grows. Commonly, most growth and yield studies in mixed-species stands implicitly understand their species proportions as the part of the stand's area which is occupied by the respective species.

The simplest way of proportioning the area at stand level would be to calculate the ratio of the species' stem numbers, basal areas, or volumes. However, these approaches do not take into account that the species may have different growing space requirements (cf. R o and Sterba 2009; Dirnberger and Sterba 2014). A first approach dealing with this problem is based on relating the observed volume of the species to their potential volume derived from yield tables (von Laer, cit. Prodan 1959). However, these reference values are not necessarily good indicators for growing space since yield tables usually do not present maximum densities for species. This is why species proportions in general should consider the growing space requirements, i.e. maximum density of the respective species in the mixed stand.

The different potentials of each species are best described by potential basal area or potential stem number. R o et al. (2016) point out that this only results in reliable and unbiased species proportions, if the potential stand density (i.e. maximum density) of the observed species in the particular location is known.

The idea of using potentials of growth parameters for estimating species proportions is based on the following considerations (Sterba 1998): According to the "rule of

three” the ratio of the basal area per hectare of a species in a mixed stand and the basal area of the same species in a monospecific stand at maximum density gives the area of a stand with maximum density and the observed basal area. The sum of these areas for all species is then the hypothetical area of a fully stocked mixed stand, keeping in mind that the occupied area of each species is the target variable. Subsequently, one could determine species proportions by calculating the fraction of this hypothetical area which the species occupy (for details, see Eqs. 1 and 2 in “Materials and methods” section).

For growth comparisons of a species in a mixed and a monospecific stand, this definition of proportions by area is conclusive and adequate, provided that the used measure of potential density for each species is correct (Dirnberger and Sterba 2014; Huber et al. 2014; Sterba et al. 2014). Finding the correct potential density is a considerable challenge in forestry. Usually, densities denoted in yield tables are used as reference for potential density, despite the underlying specific stand treatment (thinning approach), which of course reduces stand density below the potential (i.e. maximum) stand density. For the sake of completeness, it has to be mentioned that there are yield tables which explicitly indicate maximum density based on unthinned experimental plots (Lembcke et al. 1977; Dittmar et al. 1986), but aside of information regarding the site index, they require a stand specific yield level (Assmann 1970) to be applied correctly. This yield level as a measure for potential density is not known in most cases.

Several studies measured fully stocked neighboring monospecific stands on similar sites and used them as reference for potential growth and density (e.g. Pretzsch 2009; Pretzsch and Schütze 2009; Dirnberger and Sterba 2014). The idea originates from Assmann’s (1970) concept of the maximum basal area, which is the basal area of an unthinned even-aged monospecific stands. Thus, by using the basal area of unthinned monospecific stands stocking on similar sites would serve as appropriate measure for the potential stand density. For Norway spruce (*Picea abies* L. Karst.) and European beech (*Fagus sylvatica* L.) Dirnberger and Sterba (2014) showed that the estimation of the mixture proportions using the basal area of neighboring monospecific stands delivered satisfying results for evaluating the growth efficiency, if the appropriate maximum density for each species was represented by the monospecific stand.

Charru et al. (2012) and Hann (2014) pointed out that it may be difficult to find such neighboring reference stands in temporary plots representing the maximum density, because the management history in temporary plots is often not known. In other words, with increasing stand age it is increasingly unlikely to find reference stands that represent the maximum density.

Another option for estimating potential density would be a density index. Waskiewicz et al. (2013) stated that a measure of stocking, like the relative density index (RDI), could also serve as appropriate measure for comparing mixtures and neighboring monospecific stands. According to Hein and Dhôte (2006) the relative density index relates actual stem number to its potential stem number and therefore can take different mean tree sizes into account. To obtain the potential stem number, appropriate models for the maximum density line have to be found, according to Reineke (1933). Several studies developed such models, e.g. Schnedl (2003) for European beech and Scots pine (*Pinus sylvestris* L.) in Austria, or Döbbeler (2004) for several tree species in Germany, and Condés et al. (2016) for Scots pine and European beech stands in Europe depending on the aridity index according to de Martonne (1926). These models showed considerable differences for this relationship between tree species and between mixed and monospecific stands at the same sites (Pretzsch and Biber 2016). Among others, these differences are related to site properties, e.g. Condés et al. (2016) found higher potential densities for Scots pine than for European beech in young stands on sites with low humidity while the maximum stand density of European beech exceeded that of Scots pine in older stands. On humid sites, opposite relationships were found.

When evaluating growth efficiency of species at the individual tree level, growth is commonly related to crown projection area (Assmann 1970) or leaf area (Waring et al. 1980; O’Hara 1988; Gspaltl et al. 2012, 2013). Pretzsch (2006) stated that a part of the stand area has to be assigned to each tree to be able to upscale growth efficiency from tree level to stand level. Hence, area proportioning has to be carried out at individual tree level for this purpose. Such a tree-level approach for determining species proportions is based on the fraction of the stand area which is available for each tree. The used crown measures should be able to describe this available area for each tree in dependence of the tree size. Assuming that light is the limiting factor at a given site, growth characteristics like crown projection area or leaf area should be used to represent the occupied area in terms of growing space. The very widely used but rarely published way to estimate the fraction of the stand area occupied by a species (Mantel 1959; Hasenauer 2004) is assuming that the proportion by area is sufficiently approximated by the proportion of the canopy (i.e. crown projection area), usually estimated by ocular taxation.

While crown projection area and leaf area do not take the spatial distribution of the trees into account, the calculation of area potentially available does. The consideration of spatial information is based on the assumption that given the same crown measures a tree which occupies a large growing space is not as efficient (in terms of growth

efficiency) compared to a tree occupying a smaller growing space even if both trees get the same amount of light and other resources. Therefore, the relationship between the trees of a stand concerning crown projection area, leaf area, and area potentially available needs not necessarily be the same. Especially small and strongly suppressed trees may have a considerable amount of leaf area or crown projection area but a negligibly small area potentially available (cf. Gspaltl et al. 2012).

In summary, species proportions by area can generally be obtained with two different approaches, a stand-level approach and an individual tree approach. In this study, we calculated different mixing proportions, based on both approaches. For calculations of proportions at stand level, the basal area of neighboring monospecific stands and potential maximum stem numbers according to Condés et al. (2016) were applied. For the proportions calculated at the tree level, measures such as leaf area, crown projection area, or area potentially available were used.

We applied these approaches to mixed stands of European beech and Scots pine on a wide range of different sites across Europe. The objective was to identify the best stand-level method and to determine through which tree-level method—using crown projection area, leaf area, or area potentially available—this stand-level approach was best approximated.

The differences in proportions from the stand-level and the tree-level approaches were evaluated to see whether the approximations based on crown measures were appropriate. This would only be the case if the species proportion from the stand-level approach did not differ from the tree-level approach. In more detail, (i) the proportions of the stand-level approach should be highly correlated with those of the individual tree-level approach; (ii) the difference between the two approaches should be zero for (a) the whole range of proportions and (b) the full range of observed stand ages. Since proportion estimation based on crown projection area is most commonly used in forest practice, this comparison is of high relevance, and thus, we wanted to show whether this approximation remains recommendable in the future.

Materials and methods

Experimental sites

During the COST action FP1206—EUMIXFOR, a set of 32 triplets consisting of pine–beech mixtures and neighboring monospecific stands of Scots pine and European beech were established along a productivity gradient throughout Europe (Pretzsch et al. 2015). According to jointly compiled instructions on data collection, the triplets had to be set up in even-aged, mono-layered stands, which had not

undergone thinning or experienced disturbances during the last decades (and therefore being fully stocked). For each given triplet, all three stands had to be on similar soil substrate, with comparable aspect and slope. The mixed stands were to consist of a single-tree mixture, i.e. the two species were not to be mixed as groups of one species mixed with groups of the other species. Once established, diameter, total height, and crown base height were measured for all trees of each plot. Optionally, tree coordinates and crown projection areas were to be measured.

We used 25 out of the 32 triplets, because crown measurements were not taken on the remaining seven triplets. Most frequently, the crown radii were measured in eight cardinal directions (from north to northwest). In a few cases, there were just 4 or 6 crown radii per tree measured. The main challenge of these crown measurements is to correctly identify the crown edge. Measurements were taken by walking in prescribed directions, tangential to the perimeter of the crown. Within one of the 25 triplets, no coordinates of the trees were measured. This triplet was not used for the approaches considering the spatial distribution (area potentially available, see below).

A total of 6491 trees were recorded at an elevation ranging from 20 to 1290 m above sea level. The precipitation on the 25 triplets ranged from 520 to 1175 mm, and the mean annual temperature varied from 6 to 10.5 °C. Therefore, the aridity index according to de Martonne (1926), calculated as ratio of precipitation and mean temperature plus 10°, was determined to be within a range of 28–61 mm °C⁻¹. Stand age, soil characteristics, climate data, and site information can be found in the online supplement material of Pretzsch et al. (2015). Mean plot characteristics of the 25 triplets are given in Table 1.

Species proportions at the stand-level approach

For estimating proportion by area (*prop*) with the stand-level approach, we used the ratio between observed basal area (*BA*) and potential basal area for each species (*i*) divided by the sum of the ratios of all species (Eq. 1).

$$prop_{BA} = \frac{BA_i/BA_{i,neighbor}}{\sum BA_i/BA_{i,neighbor}} \quad (1)$$

Since the basal area potential was assumed to be the respective basal area of the neighboring monospecific stands at the triplet ($BA_{i,neighbor}$), this stand-level method is referred to as “Neighbors.”

The same calculation (Eq. 1) can be done by using maximum basal area ($BA_{i,max}$) as potential value of basal area. Equation 2 shows its equivalence to the relative density index (*RDI*), which is the ratio of observed (N_i) to maximum stem number ($N_{max,i,dg}$) at given mean diameter (*dg*) for each species.

Table 1 Mean and range (in brackets) of characteristics of the measured triplets. Stand variables are stem number (N), basal area (BA), quadratic mean diameter (dg), and crown projection area (CPA)

Species	Plots	Age (years)	Martonne (mm C ⁻¹)	N (trees ha ⁻¹)	BA (m ² ha ⁻¹)	dg (cm)	CPA (m ² m ⁻²)
Sc. pine + E. beech	25	68.7 (35–150)	40.3 (28.0–61.1)	1138 (223–2681)	41.9 (19.1–79.5)		0.97 (0.16–2.16)
Sc. pine mixed	25			455 (39–1609)	23.2 (7.0–43.8)	28.7 (13.7–57.8)	0.50 (0.16–1.08)
E. beech mixed	25			682 (127–1972)	18.6 (10.9–36.6)	23.3 (11.1–47.0)	1.44 (0.79–2.16)
Sc. pine monospecific	25			1084 (104–3527)	41.4 (16.0–63.3)	27.1 (13.7–45.1)	0.98 (0.38–1.89)
E. beech monospecific	25			1171 (207–3569)	35.4 (18.1–54.4)	24.3 (10.7–50.7)	2.10 (1.13–3.24)

$$prop_{BA,i} = \frac{BA_i/BA_{i,max}}{\sum BA_i/BA_{i,max}} = \frac{\frac{N_i \cdot dg_i^2 \cdot \pi/4}{N_{max,i} \cdot dg_i^2 \cdot \pi/4}}{\sum \frac{N_i \cdot dg_i^2 \cdot \pi/4}{N_{max,i} \cdot dg_i^2 \cdot \pi/4}} = \frac{\frac{N_i}{N_{max,i,dg}}}{\sum \frac{N_i}{N_{max,i,dg}}} = \frac{RDI_i}{\sum RDI_i} = prop_{RDI,i} \tag{2}$$

According to Condés et al. (2016), we calculated the maximum stem number (N_{max}) for each species as a function of the quadratic mean diameter of the mixed stand (dg in cm) in dependence of the Martonne index (M in mm °C⁻¹). We took their parameters for the maximum density line, which Condés et al. (2016) calculated by quantile regression for the 95th percentile using data from national forest inventories across Europe resulting in different models for Scots pine (Eq. 3) and European beech (Eq. 4).

$$N_{max,pine} = (339,979 - 2,764.14 \cdot M) \cdot dg_{pine}^{(-1.9662 + 0.0065 \cdot M)} \tag{3}$$

$$N_{max,beech} = \exp(10.9 + 0.03 \cdot M) \cdot dg_{beech}^{(-1.2716 - 0.0091 \cdot M)} \tag{4}$$

This second stand-level method is hereafter referred to as “RDI.”

Species proportions at the tree-level approach

The methods for estimating species proportions by area at tree level are based on the ratio between the sum of a growth parameter of each tree for a given species and the sum of this parameter for all species. Among the available growth parameters such as diameter, height, and crown length, we used those which may represent space occupation best. We assumed that light availability is the limiting factor at a given site. Therefore, we used crown projection area and leaf area as growth parameters. Using crown projection area results in Eq. 5.

$$prop_{CPA,i} = \frac{\sum_{j=1}^{n_i} CPA_{ij}}{\sum_i \sum_{j=1}^{n_i} CPA_{ij}} \tag{5}$$

The crown projection area (CPA) is summed up for species i for tree $j = 1$ to n (number of individuals of either species). Dividing this sum by the total sum of all crown projection areas for all species gives the proportion for species i .

Analogously using leaf area (LA) results in Eq. 6.

$$prop_{LA,i} = \frac{\sum_{j=1}^{n_i} LA_{ij}}{\sum_i \sum_{j=1}^{n_i} LA_{ij}} \tag{6}$$

The leaf area used in Eq. 6 was derived from published allometric functions (see “Leaf area estimation” section).

Because these measures do not take the spatial distribution of the trees into account, we additionally calculated area potentially available. Therefore, we carried out a weighted Voronoi tessellation (or Voronoi diagram) to account for differences in tree size. The whole plot is divided into small pixels, and each pixel is attributed to that tree for which d_j^2/w_j is minimum, where d_j is the distance between pixel and tree j and w_j is the weight characterizing the growth parameter (crown projection area or leaf area, respectively) as indicator for space occupancy (for details, see Gspaltl et al. 2012). Proportions can then be calculated analogously to Eqs. 5 and 6 for the resulting area potentially available (APA) (Eq. 7).

$$prop_{APA,i} = \frac{\sum_{j=1}^{n_i} APA_{ij}}{\sum_i \sum_{j=1}^{n_i} APA_{ij}} \quad (7)$$

Because of missing information about neighborhood, the area potentially available for border trees in each stand could not be calculated, so these trees were not considered for further calculations.

Leaf area estimation

Following Thurnher et al. (2013), we did not use models with tree diameter as sole predictor because their reliability is limited—especially for larger diameters. So we compiled functions for leaf area depending on at least one additional predictor next to diameter.

For Scots pine, we used two equations for all triplets which also take crown parameter into account, one suggested by Eckmüller (2006) (Eq. 8) and another one by Socha and Wezyk (2007) (Eq. 9). In both studies, needle mass was modeled using diameter at breast height (*dbh* in cm), tree height (*h* in m), and crown ratio (*cr* in m/m, calculated as crown length divided by tree height). Leaf area (*LA*) was finally calculated by applying specific leaf area (*SLA*) of Scots pine, which Xiao et al. (2006) estimated to be $4.38 \text{ m}^2 \text{ kg}^{-1}$.

$$LA_{\text{pine}} = 0.093 \cdot cr^{0.518} \cdot (dbh^2 \cdot h)^{0.559} \cdot cf \cdot SLA \quad (8)$$

$$LA_{\text{pine}} = \exp(-0.548 + 2.082 \cdot \ln dbh - 1.473 \cdot \ln h - 0.716 \cdot \ln(1 - cr)) \cdot cf \cdot SLA \quad (9)$$

where *cf* is the correction factor with a value of 1.051 and 1.053, respectively, as reported by Eckmüller (2006) and Socha and Wezyk (2007). The correction factor accounts for the bias when using double-logarithmic regression analysis.

For European beech, we also used a general model for all triplets, according to Gspaltl and Sterba (2011) (Eq. 10). They suggested an equation for calculating leaf area (*LA* in m^2) based on crown surface area (*CSA* in m^2),

diameter at breast height (*dbh* in cm), and the dominant height (h_{dom} in m). We used the quadratic mean of the measured crown radii and crown length for estimating crown surface area, following the crown model of Pretzsch (2009). The correction factor (*cf*) here took a value of 1.051.

$$LA_{\text{beech}} = \exp(-1.87 + 1.15 \cdot \ln CSA - 0.885 \cdot \ln(h_{\text{dom}}/dbh)) \cdot cf \quad (10)$$

Thus, the proportions by leaf area were calculated using the equation for leaf area of European beech, according to Gspaltl and Sterba (2011), and two different equations for the leaf area of Scots pine (Eckmüller 2006; or Socha and Wezyk 2007, respectively) to test for an effect of using different leaf area equations on species proportions.

Statistical analysis

We only focused on Scots pine proportions because in a two-species mixture the proportion of the second species, in our case beech, is the completion to 1. Statistical tests would give the same results whatever species is taken.

To investigate the relationships between the individual tree approaches and each stand-level approach, several tests were conducted. We applied linear regression models using the proportions of each method of leaf area, crown projection area, and area potentially available as independent variable with each stand-level method as predictor, proportions from the “Neighbors” and from the “RDI” approaches, respectively. The coefficients of determination of the regressions were tested to see if there was any significant relationship between the tree-level and stand-level approaches at all. Otherwise, further testing would be unnecessary.

Simultaneous *F*-tests were then conducted to test the hypothesis that the tree-level proportion is a linear model of the stand-level approach with an intercept equal to 0 and a slope equal to 1. Differences in means (Δ) were tested by pairwise Student’s *t*-tests for the hypothesis that the true difference of proportions at tree level minus proportions at stand level is 0.

Taking the large age range (from 35 to 150 years) into account, the density in the neighboring monospecific stands may have been reduced (e.g. by thinning or any other disturbances). On the older plots, such a density reduction could possibly not be recognized anymore when the plots were selected. Therefore, we investigated the effect over age while using different potentials for estimating species proportions. This was also done by applying linear regressions for the differences between individual tree-level and stand-level approaches in dependence of age and testing the coefficients of determination. The underlying

hypothesis was that age does not affect the estimations for species proportion.

Results

First, we analyzed the correlation of the tree-level and the stand-level approaches using proportions from “Neighbors” as reference. We found that all leaf area and area potentially available methods as well as the crown projection area method were highly significant, or at least significantly correlated with the method “Neighbors” (Table 2), keeping in mind that we just analyzed proportions of pine because those of beech would be the completion to 1.

The crown projection area method showed rather high deviations from the stand-level approach. The difference of the means (Δ) for proportions by crown projection area minus proportions by “Neighbors” is -0.252 , meaning a 25.2% lower proportion of Scots pine on average for this tree-level method (Table 2; Fig. 1a). In contrast, fewer deviations from the stand-level approach were observed for the leaf area methods. The smallest deviations were found for the leaf area method “LA(SochaGspaltl)”. Using the area potentially available at tree level did not substantially improve the relationships (Fig. 1b; Table 2).

Simultaneous F -tests gave evidence that only the leaf area method “LA(SochaGspaltl)” showed non-significant deviations from the stand-level approach.

The coefficient of determination and the level of significance as well as the test on deviations would lead to favoring the leaf area method “LA(SochaGspaltl)”.

However, differences to the method “Neighbors” were significantly correlated with age (Fig. 2, left part). While the crown projection area method was not at all correlated with age, the leaf area methods were. The differences increased with increasing age. The same was true for the area potentially available methods when weighting them with the different leaf area equations mentioned above.

Thus, we suggested that taking neighboring monospecific stands as reference was increasingly wrong with increasing stand age. To eliminate the age trend, we used RDI which considers the quadratic mean diameter as a surrogate for age. According to Condés et al. (2016) this potential was calculated in dependence of the Martonne index. Using this “RDI” method, the relationship with age was not significant anymore for leaf area and area potentially available methods (Table 3; right part of Fig. 2).

Higher correlations for tree-level methods were achieved by using “RDI” instead of “Neighbors”, and the coefficient of determination was up to 25% higher (Table 3).

“RDI”-based models showed narrower confidence intervals than the “Neighbor” method (compare Fig. 1a and 1b to 1c and 1d). Thus, the estimations were more accurate, but significant deviations to the stand-level approach were more likely. While all methods showed highly significant correlations, the simultaneous F -test indicated non-significant deviations for the leaf area method “LA(SochaGspaltl)”. Consequently, this model was not significantly deviating from the “RDI” model, indicating that this tree-level method is the best approximation for the “RDI” method. This finding was also

Table 2 Statistics for the relationships between the Scots pine proportions derived from the tree-level methods and those by the stand-level approach with the neighbors as potentials: *LA(EckGspaltl)* is the species proportion by leaf area according to Eckmüller (2006) and Gspaltl and Sterba (2011), *LA(SochaGspaltl)* is analogous, but using leaf area of Scots pine according to Socha and Wezyk (2007), and *CPA* is proportion by crown projection area. *APA(EckGspaltl)*, *APA(SochaGspaltl)* and *APA(CPA)* are proportions by area potentially available using different weights (the two above-mentioned combinations of leaf area or crown projection area, respectively). R^2

is the coefficient of determination of the regression between the Scots pine proportions by the two methods, and $p > F_{\text{simult}}$ is the significance of the simultaneous F -test, indicating that the linear relationship between the two ways of estimating the proportions deviates from the 45°-line (Fig. 1). Δ is the mean difference between the two respective proportions, $p > \Delta$ is the significance of the respective pairwise t -test, $R^2 \Delta \sim \text{age}$ is the coefficient of determination for the regression between the difference Δ and the stand age, and $p > R^2 \Delta \sim \text{age}$ is the respective significance

Stand-level approach	Tree-level method	Triplets	R^2	$p > R^2$	$p > F_{\text{simult}}$	Δ	$p > \Delta$	$R^2 \Delta \sim \text{age}$	$p > R^2 \Delta \sim \text{age}$
“Neighbors”	LA(EckGspaltl)	25	0.372	0.0012	0.0004	-0.109	0.0001	0.278	0.0067
	APA(EckGspaltl)	24	0.405	0.0001	0.0000	-0.118	0.0000	0.307	0.0049
	LA(SochaGspaltl)	25	0.565	0.0000	0.4417	-0.023	0.2302	0.278	0.0067
	APA(SochaGspaltl)	24	0.459	0.0003	0.0307	-0.049	0.0266	0.275	0.0085
	CPA	25	0.627	0.0000	0.0000	-0.252	0.0000	0.000	0.9737
	APA(CPA)	24	0.569	0.0000	0.0000	-0.226	0.0000	0.092	0.1507

Significance levels: significant $p < 0.05$; high significant $p < 0.01$; highly significant $p < 0.001$

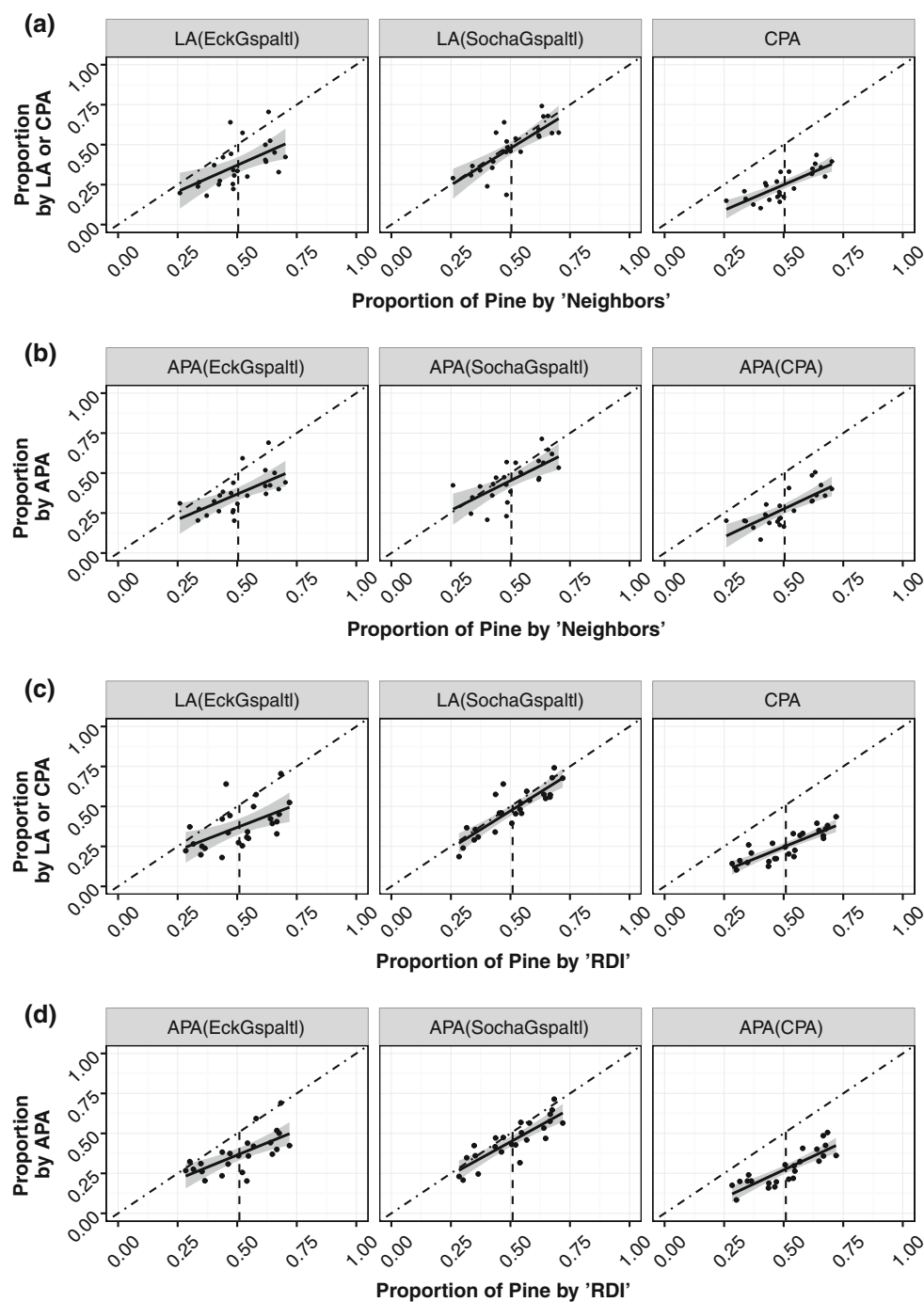


Fig. 1 Comparison of the proportions on individual tree level to the ones on stand level using potentials from neighboring monospecific stands (“Neighbors”, **a** and **b**) and from relative density index (“RDI”, **c** and **d**). Leaf area and crown projection area methods do not consider spatial distribution of trees (**a** and **c**), whereas area

potentially available methods do (**b** and **d**). *Dash-dotted lines* indicate a perfect fit, *dashed lines* the respective means of stand-level approaches, and *solid lines* the fitted linear models with their respective confidence intervals; for abbreviations see Table 2

supported by the test on differences in means, which resulted in a non-significant Δ for the “RDI”- to that leaf area- method.

To further investigate the age effect, we used the neighboring monospecific stands for each species of each

triplet. The basal areas of these stands were compared to the maximum basal areas derived from the maximum stem number according to Condés et al. (2016) and plotted over age (Fig. 3). Interestingly, the trend for the ratios between the respective basal areas was steeper and significant just

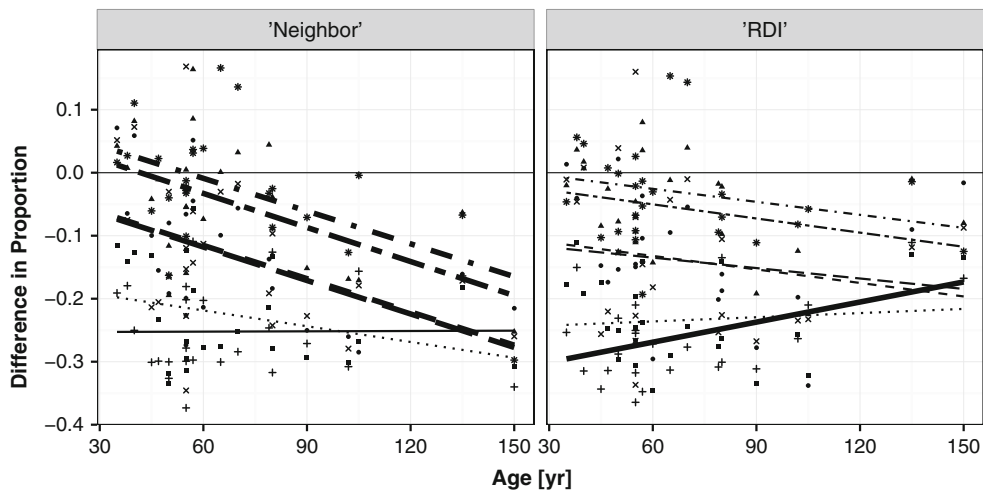


Fig. 2 Difference in tree species proportions between tree-level versus stand-level approaches as a function of stand age, using the potential density from “Neighbors” (left) and “RDI” (right). The tree-level methods and their associated regression lines are APA (CPA) (squares and dotted lines), APA(EckGspaltl) (circle and long-

dashed line), APA(SochaGspaltl) (triangle and two-dashed line), CPA (plus and solid line), LA(EckGspaltl) (cross and dashed line), and LA(SochaGspaltl) (star and dot-dashed line). Significant regression lines are bold; for abbreviations see Table 2

Table 3 Statistics for the relationships between the Scots pine proportions derived by the tree-level methods and those by the stand-level approach with potentials from the relative density index depending on the Martonne index (“RDI”). For abbreviations see Table 2

Stand-level approach	Tree-level method	Triplets	R^2	$p > R^2$	$p > F_{simult}$	Δ	$p > \Delta$	$R^2 \Delta \sim age$	$p > R^2 \Delta \sim age$
“RDI”	LA(EckGspaltl)	25	0.408	0.0006	0.0001	-0.114	0.0001	0.052	0.2734
	APA(EckGspaltl)	24	0.514	0.0001	0.0000	-0.124	0.0000	0.051	0.2867
	LA(SochaGspaltl)	25	0.740	0.0000	0.1618	-0.028	0.0656	0.045	0.3075
	APA(SochaGspaltl)	24	0.714	0.0000	0.0020	-0.055	0.0014	0.054	0.2747
	CPA	25	0.712	0.0000	0.0000	-0.257	0.0000	0.231	0.0151
	APA(CPA)	24	0.711	0.0000	0.0000	-0.232	0.0000	0.025	0.4644

Significance levels: significant $p < 0.05$; high significant $p < 0.01$; highly significant $p < 0.001$

for Scots pine ($R^2 = 0.279$, $p = 0.0066$), but not for European beech ($R^2 = 0.125$, $p = 0.0830$).

Discussion

The aim of this study was to determine appropriate methods to estimate tree species proportions in two-species stands, using triplets along a gradient of sites with European beech and Scots pine mixtures across Europe. The conclusive method to determine species proportions at stand level is to estimate the potential densities of the respective monospecific stands. The methods based on potential densities according to Condés et al. (2016) performed best. In a second step, we evaluated the performance of different tree-level methods (crown projection

area, leaf area, and area potentially available) in view of approximating the proportions of the stand-level method.

At the stand level, we used estimates for potential growth to estimate species proportions by area, which also proved to be appropriate in prior studies (Río and Sterba 2009; Dirnberger and Sterba 2014; Huber et al. 2014; Sterba et al. 2014). In the course of the triplet study, each mixed-species stand of Scots pine and European beech was supposed to have fully stocked and unthinned monospecific stands of both species in direct neighborhood (Pretzsch et al. 2015). These monospecific stands were assumed to provide best possible information about the local species-specific maximum stand density. Our results show that in general the neighboring monospecific stands are able to describe potential density and thus could serve as reference for deriving the mixing proportions.

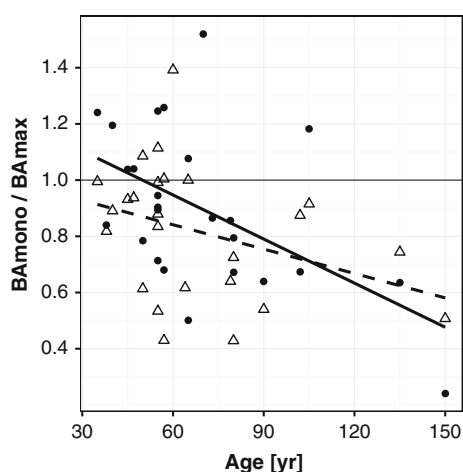


Fig. 3 Ratios of basal area observed in the monospecific stand (BA_{mono}) and the maximum basal area (BA_{max}) according to Condés et al. (2016) as a function of stand age separated by tree species. European beech is indicated by *triangle* and a *dashed* regression line, Scots pine by *filled circle* and a *solid* regression line

Our results also showed that Charru et al. (2012) and Hann (2014) were right in stating that it can be difficult to find such monospecific reference stands in every case. Mixed-species experiments often do not comprise reference stands of the respective species. Either reference plots were once available but later damaged by biotic or abiotic disturbances and therefore abandoned, or unthinned, fully stocked monospecific stands were not established at all. Therefore, estimations on potential stand density are needed.

Forrester and Pretzsch (2015) stated that maximum stand density could vary with changes in climatic conditions at a site (e.g. during drought), and they concluded that this could influence the results when studying mixing effects. Indeed, Condés et al. (2016) found that climatic conditions indicated by the Martonne index influenced maximum density. For the average Martonne index of our triplets, the maximum density lines of Scots pine and European beech are quite similar and they are also rather near to our results when using the appropriate coefficients derived by Pretzsch and Biber (2005). However, when using higher or lower Martonne indices, the relative density indices differ considerably for both species. While Pretzsch and Biber (2005) assume a constant slope of the maximum density line for a species and use the intercept as an expression of site quality, Condés et al. (2016) consider the effect of the Martonne index on both, the slope, and the intercept of the maximum density line. Therefore, we found the “RDI” to be the most appropriate method at stand level. The potential used for the “RDI” method takes the significant effect of the Martonne index on maximum stem number into account, i.e. the derived potential stand density depends on climatic conditions.

At the individual tree level, one major result was the better performance of the leaf area-based methods compared to the crown projection area method, irrespectively if these measures were used directly or as a weight to calculate the area potentially available. The proportions by crown projection area were far beyond the perfect approximation of any stand-level approach. This finding is in line with the findings of Dirnberger and Sterba (2014) for Norway spruce and European beech mixtures. They found that the leaf area method and the method “area potentially available weighted by leaf area” were the most appropriate estimation for species’ proportions. This may be generally explained by the fact that leaf area is the physiologically more meaningful parameter for describing growing space (O’Hara 1988). This explanation may also be valid for the mean deviation between the leaf area methods and the stand-level approaches which was close to zero. These deviations were therefore even non-significant for the estimations of leaf area using the models according to Socha and Wezyk (2007) and Gspaltl and Sterba (2011).

While Dirnberger and Sterba (2014) found that the proportions calculated from the area potentially available better reflect the species proportions derived from the stand-level approach, this study found that the proportions by area potentially available showed poorer correlations than the proportions by leaf area. This was also indicated by higher differences and by significant deviations according to the simultaneous F -tests. This difference might be caused by the sample size resulting in a considerable amount of border trees. As mentioned above, these border trees were not considered for calculating the available area. Thus, the population of the trees, for which the area potentially available could be calculated, was not the same as the population of all trees on the plot.

At this stage, it is worthwhile to mention one limitation of our study that is immanent of any tree-level approach. Since the growth of individual trees in mixed stands is not yet investigated in every detail, no one can precisely say where the growing space borders between trees are. Especially the rooting systems of different trees might overlap and share the same growing space. Thus, in all tree-level approaches the borders have to be defined more or less arbitrarily. This is particularly true for the area potentially available methods. However, a good match of the species proportions with the stand-level approach is an indicator for a reasonable choice of the individual tree growing space definition.

In summary, the high similarity of the resulting species proportions between the leaf area method “LA(SochaGspaltl)” and the stand-level approach was confirmed by high correlations as well as non-significant deviations and mean differences of the proportions between both levels. However, using potentials from neighboring monospecific

stands at the stand level resulted in a significant age trend of these differences. The age trend disappeared when applying potentials according to Condés et al. (2016). A possible explanation for this finding was already mentioned above. According to Charru et al. (2012) and Hann (2014), it might have been difficult to find appropriate reference monospecific stands to obtain maximum density especially when investigating temporary plots. The comparability of the site conditions of reference monospecific stands can surely be judged best on-site. However, with increasing age the knowledge of the management history becomes less reliable.

Obviously, the neighboring monospecific stands did not sufficiently reflect the differences in potential growth for each species in this study. This finding is hard to explain as triplet stand selection should only comprise fully stocked stands. However, it might be that some of the monospecific stands were repeatedly thinned or have suffered from abiotic or biotic damage in the past. In contrast, the Martonne index seems to be able to describe potential density more reliable for these two species for a wide range of sites in Europe. Interestingly, using neighboring monospecific stands for estimating potential stand density but not “RDI” resulted in an age trend for the differences in proportion between the leaf area methods and the stand-level approaches. Thus, we had to reject the hypothesis that the assumption for potentials by “Neighbors” is independent of age.

Pretzsch et al. (2016) found that important crown measures (e.g. crown ratio) are significantly affected by mixture and also by water availability. Keeping in mind that our leaf area estimations are based on several crown measures, this could serve as another plausible explanation for the almost perfect fit of the leaf area method with the stand-level approaches. Additionally, the dependency on water availability of the crown architecture may be the reason for the disappearance of the age trend when comparing the leaf area methods and the “RDI” method, which also depends on Martonne’s aridity index.

While looking at the age trend for each species separately, we also found decreasing age trends for the ratios of observed basal area to maximum basal area (Fig. 3). However, the correlation was only significant for Scots pine. One reason for this may be the higher susceptibility of Scots pine towards snow break, because the snow load on conifer crowns is many times that of broadleaves (Nykänen et al. 1997). Thus, it is possible that snow break occurred in the older Scots pine stands some time ago and was not noticed while assigning the monospecific reference stands and could explain why in this study the stand-level approach with the potential density taken from the “RDI” performed better.

Conclusions

We found that every definition of species proportion by area of European beech and Scots pine in mixed stands following the stand-level approach should be based on an estimation of potential density. As climate impacts the potential density of European beech and Scots pine, reliable estimations of species proportion have to be derived from potential densities which take the climate conditions into account. Thus, an appropriate estimation would be to calculate proportions by area using the relative density index with maximum stem number in dependence of climatic indexes like the Martonne aridity index (see Condés et al. 2016).

We also found that approximations of proportions by area at individual tree level should better rely on leaf area (“LA(SochaGspaltl)”) than on crown projection area. While working with Norway spruce and European beech, Dirnberger and Sterba (2014) came to the same conclusion, but their dataset was rather small and just locally valid. The present study validated these relationships for a much larger sample size and wider range of sites across Europe. Our results clearly show that species proportions by crown projection area do not represent species proportions by area. Considering this, it should be kept in mind that the most common way in forest practice to derive the share of crown projection area by ocular estimations would lead to even more imprecise and biased results.

Considering the fact that forest managers usually have data at stand level only, the use of the above-mentioned stand-level methods which take into account species-specific potentials for density is highly recommended for calculating mixture proportions for mixed stands of European beech and Scots pine across Europe. The elucidation of more precise estimations of mixing proportions will help to prevent forest managers as well as scientists from misinterpretations concerning productivity and other ecosystem services of mixed stands compared to monocultures.

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