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Characterization of the structure, dynamics, and productivity of mixed-species stands: review and perspectives

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Abstract The growth and yield of mixed-species stands has become an important topic of research since there are certain advantages of this type of forest as regards functions and services. However, the concepts and methods used to characterize mixed stands need to be understood, as well as harmonized and standardized. In this review we have compiled a set of measures, indices, and methods at stand level to characterize the structure, dynamics, and productivity of mixed stands, and we discuss the pros and cons of their application in growth and yield studies. Parameters for the characterization of mixed stand structure such as stand density, species composition, horizontal (intermingling) and vertical tree distribution pattern, tree size distribution, and age composition are described, detailing the potential as well as the constraints of these parameters for understanding resource capture, use, and efficiency in mixed stands. Furthermore, a set of stand-level parameters was evaluated to characterize the dynamics of mixed stands, e.g. height growth and space partitioning, self- and alien-thinning, and growth partitioning among trees. The deviations and changes in the behaviour of the analysed parameters in comparison with pure stand conditions due to inter-specific interactions are of particular interest. As regards stand productivity, we reviewed site productivity indices, the growth–density

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relationship in mixed stands as well as methods to compare productivity in mixed versus monospecific stands. Finally, we discuss the main problems associated with the methodology such as up-scaling from tree to stand level as well as the relevance of standardized measures and methods for improving forest growth and yield research in mixed stands. The main challenges are also outlined, especially the need for qualitatively sound data.

Keywords Stand structure indices · Growth pattern · Self- and alien-thinning · Maximum density · Site productivity indices · Mixing effect

Introduction

Although far-from-nature monocultures were of high interest in Europe in the past, today, close-to-nature mixed tree species stands are receiving more and more attention as many studies have highlighted the importance of species diversity for most forest functions and services (Knoke et al. 2008; Jactel et al. 2009). Promoting mixed forests has also been identified as an adaptation strategy in forest management to cope with climate change (Bolte et al. 2009; Kolström et al. 2011). This reality involves a greater demand for knowledge regarding mixed forest dynamics and management practices, which in turn has led to an increasing number of studies focusing on the effect of species composition on forest dynamics, growth, and yield, as well as on the effect of silvicultural treatments on these forests (Bravo-Oviedo et al. 2014).

Decades of research in pure stands have yielded standards for characterizing their structure [e.g. Kraft's social classes, Reineke's stand density index (1933)], dynamics (e.g. self-thinning), and productivity (e.g. growth–density curves), as well as providing an indication of their performance through simple phytometric methods (e.g. site index). This standardization of terminology (Helms 1998), symbols (van Soest et al. 1965), establishment of experiments (Skovsgaard et al. 2006), and measurement (Prodan 1968), along with the evaluation and reporting of results (Johann 1993) is important in order to achieve comprehensive evaluation, comparison, and communication in the science of forest growth and yield.

However, the great variability in mixed forest structure and functioning, together with the lack of harmonized concepts and methods related to growth and yield, leads to a number of difficulties when comparing and generalizing results from research studies (Forrester and Pretzsch 2015). Various aspects have been covered by individual scientific contributions, e.g. species proportion (Assmann 1954; Dirnberger and Sterba 2014), stand density (Sterba and

Monserud 1993; Ducey and Knapp 2010), or experimental designs (Kelty and Cameron 1995; Vanclay 2006), as well as a general overview of characterization and methods for evaluation reported by Pretzsch (2009). However, there is still a need for a complete, comprehensive set of measures, indicators, and methods for the evaluation of forest dynamics, growth, and yield in mixed stands.

Many of the available measures and methods use monocultures as a reference for characterizing mixed stands. Even-aged, mono-specific stands which are often artificially regenerated can be a questionable point of reference when used in comparison with more natural mixed stands. Nevertheless, monocultures are useful benchmarks as they often represent the silvicultural "business-as-usual". Mixed stands are often only implemented if they display certain advantages over the reference stands.

The objective of this paper is to review a set of concepts for characterizing the (1) structure, (2) dynamics, and (3) productivity of mixed stands through simple practical measures. We describe the main methods and indices, focusing on stand level, and we discuss the different perspectives and implications of their use. As we focus on mixed stands we considered the total stand and the species levels. Individual tree characteristics are not considered, nor are indices for describing larger scales. Working at stand level, we attempt to describe complex spatial and temporal patterns frequently found in mixed forests, using simple measures which allow the stand dynamics and yield to be analysed in a comprehensive but at the same time comparable way. We focus our review on the application of these measures, indicators, and methods in the research of stand dynamics and productivity. The paper in hand is part of the review series in memory of Assmann, who was a German pioneer in forest production ecology and quantitative silviculture of pure and mixed-species stands (Pretzsch et al. 2015a).

Characterization of mixed stands structure

In mixed stands, inter- and intra-specific interactions occur between each reference tree and its immediate neighbours, making up—according to Schütz (1999)—a competitive entity. Growing space or growing area is often used in growth and yield sciences as an unspecific substitute for characterizing the resources of trees and stands, and analogously, the supply, capture, and use efficiency of resources (e.g. how much space is available, how much space is captured, how much a tree or stand produces per captured space). Thus, the question of how different tree species occupy growing space (horizontally and vertically) in mixed stands is crucial to understand their dynamics and

structure. Stand structure is usually described by density, size distributions, and horizontal and vertical tree distribution patterns; however, age composition might also have a strong influence on stand structure and dynamics. There are also some indices which combine several attributes of stand structure in the same index (Jaehne and Dohrenbusch 1997; McElhinny et al. 2005; Gadow et al. 2012). Below we present a set of indices describing the different stand structure attributes (Table 1).

Stand density

Density is a general concept in ecology for quantifying the abundance of a species per unit area in an ecosystem. In forestry, stand density is a term used to describe tree cover or crowding. Density is related to site occupancy, expressing the amount of resources used by trees in relation to the resource capital of a site (Dean and Baldwin 1996), e.g. in terms of growing area, and therefore to tree volume, biomass, growth, and survival.

Numerous absolute measures have been used in pure stands to reflect density, which can be directly used in mixed-species stands without modification. The easiest to measure are stem number and basal area per unit area. Volume and biomass are measures which are of particular interest to forest managers and are important with regard to physiological issues (carbon assimilation). However, any allometric relationships used to estimate tree volume or biomass from tree diameter and height measures in mixed stands must reflect past mixture effects on tree growth and form, otherwise they might be biased. These absolute measures are easily estimated and interpreted, so they can be useful for a general stand description although their use is limited by the fact that the maximum (or other reference condition) depends on site conditions and stand development stages.

Leaf area index (LAI) is also a density variable related to canopy closure. O'Hara et al. (2001) studied the leaf area allocation in different species to improve LAI estimations for use as a stocking index in mixed stands. This measure is often used in process-based models, but it has the disadvantage of being very difficult to estimate reliably.

Density measures which relate growing space utilization to tree size are needed to compare stands of different ages or at different sites. A number of relative measures include ratios of crown length or diameter to tree height, or intertree spacing to tree height (Nieuwenhuis 2000). However, the most common measure is the stand density index (SDI) proposed by Reineke (1933), which relates tree number and mean diameter. It is based on the allometric relationship between these two variables and indicates the tree number for a reference quadratic mean diameter. As there is a maximum tree occupancy in any given area, the maximum

SDI expresses the so-called size–density relationship or self-thinning rule (see "Course of growth, yield and standing stock at tree species and stand level" section). The SDI was initially developed for pure even-aged stands, but adaptations for stands with more heterogeneous structures, such as the additive stand density index (ASDI) (Long and Daniel 1990), have also been proposed. Ducey and Knapp (2010) outline an approach for extending ASDI to mixed-species stands.

Maximum densities or space occupancy of the species comprising the mixture can be very different between the species, so a given absolute value can mean a different relative density for each species. Therefore, stand density variables relative to self-thinning boundaries, usually in terms of number of trees (N/N_{max}) or basal area (BA/BA_{max}), may be more appropriate for mixed stands. The adaptation of relative density variables to mixed stands can be categorized into two types. The first type is when the maximum self-thinning boundary is already adapted to mixed stands (Woodall et al. 2011). However, the multitude of possible mixture compositions and the changes in the average competitive status of the different species over the course of the development of such stands make it difficult to determine potential densities in mixed stands through this method. The second type is when the relative density variables are calculated as a combination of relative densities in pure stands. Examples are the relative density S (Eq. 1) based on partial relative basal area for pure stands (Condés et al. 2013; del Río and Sterba 2009) or the RDI (Eq. 2) based on stem numbers (Hein and Dhôte 2006; Waskiewicz et al. 2013).

$$S = \sum BA_i/BA_{i,max} \tag{1}$$

$$RDI = \sum N_i/N_{i,max} \tag{2}$$

where BA_i and N_i are the basal area and number of stems, respectively, while $BA_{i,max}$ and $N_{i,max}$ reflect the maximum basal area and number of stems given by the self-thinning line in a pure stand of species i. Note that the relative density of the mixed stand is the sum of fully stocked areas of all the species in the stand, although no mixing effects between the species are considered. It is also important to note that the equations for BA_{max} usually depend on dominant height (Sterba 1987), while those for N_{max} depend on the mean diameter, which results in different assumptions when comparing with pure stands.

Another way to compare relative density values of different species and to calculate their value in mixed stands is by using the equivalence competition coefficients (Begon et al. 2006, pp 234–237), which are very common in ecology (e.g. Lotka 1932; Volterra 1926). For instance, from the maximum SDI of species 1 (SDI_{max1}) and species 2 (SDI_{max2}) the competition equivalence coefficients

Table 1 Indices for characterizing stand structure at stand level in mixed-species stands

Structure characteristic	Concept	Measure	Pros (+) and cons (−)	References
Stand density	Absolute stand variables by species and for the total stand per hectare	Number of stems (N), Basal area (BA), Volume (V), Biomass (W)	+Easily estimated and interpreted; +Common use in forest practice; −Dependent on site, age, and composition	Assmann (1970), Oliver and Larson (1996)
	Leaf area per unit ground surface area by species	Leaf area index (LAI)	+Closely related to light interception and primary production; −Need detailed measurements or site-/species-specific functions	O'Hara et al. (2001)
	Adaptation of relative measures (tree growing space to tree size) to mixed stands by species-specific gravity, purity of species, etc.	Stand density index (SDI), Additive stand density index (ASDI)	+Easily interpreted; +Independent of site, stand development; −Still not available for many mixtures	Woodall et al. (2005), Weiskittel et al. (2009), Ducey and Knapp (2010), Rivoire and Moguedec (2012), Reyes-Hernandez et al. (2013)
	Sum of stand density variables relative to maximum self-thinning boundaries by species	Sum of relative density index (RDI), Sum of relative basal areas (S)	+Independent of site, stand development; +Direct comparison of mixed versus pure stands; −Need to know maximum stand density of species	Hein and Dhôte (2006), del Río and Sterba (2009), Condés et al. (2013)
	Use of competition equivalence coefficients between species	Equivalence competition coefficient for SDI (e)	+Independent of site, stand development; +Direct comparison of mixed versus pure stands; −Need to know maximum stand density of species	Begon et al. (2006), Pretzsch et al. (2015)
Species proportion	Proportion estimated from common absolute stand variables by species	Proportion by number of stems (N_i/N), Proportion by basal area (BA_i/BA)	+Easily estimated and interpreted; +Common use in forest practice; −Dependent on site, age, and composition; −Biased when maximum densities of species are very different	Pretzsch (2009)
	Species growing space occupancy estimated by biomass	Proportion by biomass (W_i/W)	+Easily estimated and interpreted; +Closely related to productivity; −Biomass equations generally based on pure stand data	Pretzsch (2009)
	Species growing space occupancy estimated by basal area or SDI corrected by species-specific wood density	Proportion by corrected basal area ($BAc_i/ \sum BAc_i$), Proportion by corrected SDI ($SDIc_i/ \sum SDIc_i$)	+Easily interpreted; −Species-specific wood density generally based on pure stand data	Assmann (1970), Woodall et al. (2005), Pretzsch (2009), Ducey and Knapp (2010)

Table 1 continued

Structure characteristic	Concept	Measure	Pros (+) and cons (−)	References
	Area occupied by species based on densities relative to maximum self-thinning boundaries	Proportion by area (a_i/S) (RDI$_i$/RDI)	+Correct the bias due to differences in maximum densities between species −Need to know maximum stand density of species	Dirnberger and Sterba (2014) Huber et al. (2014) Waskiewicz et al. (2013)
Species composition	Number of species in the stand	Species richness	+Easily interpreted −Frequency of species is not considered	
	Number of species considering their frequency in the stand	Shannon–Weaver index (H) Simpson Index (1-D)	+Based on the number and frequency of species −Not possible to distinguish these two aspects, the number and frequency of species	Shannon (1949) Simpson (1949)
	Homogeneity in species frequency	Evenness (E)	+ Information about the growing space partitioning among species	Magurran (1988)
Horizontal spatial pattern	Comparison of spatial pattern with a Poisson distribution using distances	Clark and Evans' aggregation index (R) Pielou's distribution index (PI)	+Based on real tree distributions −Need tree coordinates and positioning	Clark and Evans (1954) Pielou (1959)
	Comparison of spatial pattern with a Poisson distribution using local densities measures in quadrants	Index of dispersion or Cox index (I_c) Morisita's index of dispersion (I_δ) Index cluster size (ICS) Index of patchiness (IP) Mean crowding ($\bar{\bar{X}}$) Index of cluster frequency (ICF)	+Stem coordinates not required +Provide an idea of local density variation −Results depend on the size of the quadrants	Fisher et al. (1922) Clapham (1936) David and Moore (1954) Morisita (1959) Lloyd (1967) Douglas (1975)
	Based on homogeneity in the angles between neighbour trees and subject tree	Uniform angle index (UAI)	+Provide an idea of the mean spatial symmetry of competition −Need to measure angles among trees, which is costly but without providing real tree distribution	Gadow et al. (1998) Gadow and Hui (2002)
Species intermingling	Based on the species identity of the nearest neighbour	Segregation index by Pielou (S)	+Easily interpreted (vary between −1 and 1) −Need stem coordinates	Pielou (1977)
	Based on the species identity of the neighbours	Mingling (M)	+Stem coordinates not required −Need to register the neighbour species identity −No consideration of the number of species	Füldner (1995) Pommerening (2002) Gadow et al. (2012)
	Based on the species identity of the neighbours and on the species richness	Species average spatial status (MS$_{sp}$) Tree species spatial diversity (TTS)	+Stem coordinates not required −Need to register the neighbour species identity	Hui et al. (2011) Gadow et al. (2012)

Table 1 continued

Structure characteristic	Concept	Measure	Pros (+) and cons (−)	References
Vertical pattern	Diversity index H by Shannon (1949) applied to leaf area or to tree number within height intervals	Foliage height diversity (FHD) Tree height diversity (THD)	+Good estimation of vertical canopy distribution +Correlated to habitat function −No consideration of species composition −Difficulty of measurement	MacArthur and MacArthur (1961) Kuuluvainen et al. (1996)
	Diversity index H by Shannon (1949) applied to trees by species within height intervals	Vertical species profile index (A) Standardized species profile index (A_{rel})	+Stem coordinates not required + Consideration of species composition −Dependent on the used intervals	Pretzsch (1995b) Staudhammer and LeMay (2001) Pretzsch (2009)
	Relative height differences among neighbouring trees	Height Differentiation Index (TH)	+Stem coordinates not required −Need to register the height of the neighbours −No consideration of species composition	Gadow (1993) Füldner (1995)
	Vertical gradients and distances of neighbouring trees	Structural complexity index (SCI)	+Consider also horizontal tree distribution −No consideration of species composition −Stem coordinates required	Zenner and Hibbs (2000, Zenner et al. (2015)
Size distribution	Descriptive statistics of tree size distributions by species	Minimum, mean, maximum, standard deviation, variation coefficient, skewness, kurtosis, percentiles	+Stem coordinates not required +Can be provided by species +Can be used for different tree attributes −Not aggregated in a single index	Barbeito et al. (2009) Pretzsch and Schütze (2014)
	Relative size differences among neighbouring trees	Size differentiation index (T)	+Stem coordinates not required −Need to register the size of the neighbours −No consideration of species composition	Gadow (1993) Füldner (1995)
	Degree of heterogeneity in tree sizes based on Lorenz curve	Gini coefficient (GC)	+Stem coordinates not required −No consideration of species composition	De Camino (1976) Pretzsch and Schütze (2014)
Age composition	Mean age of dominant trees by species	Dominant age (A_0)	+Need a small sample of cored trees −No provision of the real age structure	Lee et al. (2004)
	Based on the relationship between age and large size trees	Mean diameter of large trees	+No need for tree coring −No provision of real age	Ziegler (2000)

$e_{2 \rightarrow 1} = \mathrm{SDI}_{\mathrm{max}1}/\mathrm{SDI}_{\mathrm{max}2}$ and $e_{1 \rightarrow 2} = \mathrm{SDI}_{\mathrm{max}2}/\mathrm{SDI}_{\mathrm{max}1}$ can be used for converting the SDI from one species to the other, and thus for comparing mixed and monospecific stands (Pretzsch et al. 2015b).

Besides giving a standardized basis for comparing stands of different characteristics, these relative definitions have the advantage that they provide an easy method for estimating the level of competition in the stand and for defining management recommendations.

Species composition: species proportion, species richness, diversity, and evenness

Species proportion

Of all species composition indicators, species proportion is probably the most frequently used variable to describe how species occupy growing space at stand level since it is easily estimated, interpreted, and applicable in growth and yield studies as well as in forest practice. In mixed-species stands, individuals of two or more species occupy the space above and below ground in often complex spatial arrangements, which may change over time. An appropriate approach to describing species proportions would therefore be to quantify the above- and below-ground resource capture by the sum of individuals per species. In accordance with this approach, Forrester and Albrecht (2014) and Groot et al. (2014) quantified light capture by individuals of each species to study productivity in mixed stands. However, quantifying resource capture below ground at this scale has not yet been successfully addressed.

Another option is based on quantifying the proportion of the stand area occupied by each species, reducing 3D growing space into 2D (Sterba 1998; Sterba et al. 2014). While this simplification works well for one-layered stands, it might not be suitable for other stand structures such as stratified mixtures. To define the area occupied by trees of different species, assumptions must be made with regard to the area used by individual trees, since species differ in their resource use efficiency. Most species proportion indices use the ratio of the area occupied by each species (a_i). The area these trees would occupy in a fully stocked pure stand is taken as a reference, assuming the maximum density of pure stands as explained in "Stand density" section, relative to the sum of areas occupied by all species i in the plot ($\sum a_i$), where a_i can be estimated directly from Eq. 1 or Eq. 2 (Waskiewicz et al. 2013; Dirnberger and Sterba 2014; Huber et al. 2014). The method based on $\mathrm{BA}_{\mathrm{max}}$ should only be applied in mixtures where dominant height growth is unaffected by the mixture (Huber et al. 2014). In the past, yield tables have frequently been used as maximum density references for estimating

species proportion, although they do not represent the maximum stand density if they are based on thinned stands for the sites analysed (Dirnberger and Sterba 2014). Species-specific maximum density strongly affects the species proportion variable. Therefore, any errors are also transferred, leading to possible errors when comparing the yield of pure and mixed stands (see "Comparison of productivity in mixed versus monospecific stands on tree-species and stand level" section).

Among the commonly available variables, basal area is that which is most often used to derive species proportions (e.g. Puettmann et al. 1992; Vallet and Perot 2011; Toïgo et al. 2015). However, using simple ratios between stand-level variables without first calculating a_i by species might result in biased species proportions, especially in cases where the maximum density of the species in the mixture differs significantly (Pretzsch 2009, pp. 359–360; Huber et al. 2014; Sterba et al. 2014). The use of biomass or basal area corrected by species-specific wood density implicitly represents growing space and therefore can be applied to obtain similar species proportions without the estimation of a_i. This method frequently gives similar values to those of basal area to species-specific maximum basal area ratios, while crown projection areas resulted in larger bias relative to other indices (Pretzsch 2009, pp. 359–360; Dirnberger and Sterba 2014; Huber et al. 2014). Similarly, additive SDI weighted by species-specific wood density (Woodall et al. 2005; Ducey and Knapp 2010) has been used to express species-specific growing space in mixed stands. However, it has been noted that this approach does not relate actual biomass of the species to their potential biomass, but rather assumes equal biomass production of the studied species to that at a given site.

Species richness, diversity, and evenness

Species proportion implies the use of one value per species, which can result in the need to handle a large number of values in highly diverse stands. Therefore, when mixtures comprise more than two or three species, indices that summarize species composition are often preferred.

Species richness, the Shannon–Weaver index, and the Simpson diversity index (Table 1) are the most frequently used indices and are easily estimated. These indices increase with the number of species and when the trees are distributed equally among all the species, while Magurran's (1988) evenness index provides an indicator of the homogeneity in species abundance (proportion). This last index takes the maximum value of one when the species have equal abundance in the stand and is not defined in mono-specific stands.

A number of studies have addressed the relationship between tree species richness/diversity and productivity in

forests using data from regional forest inventories (e.g. Caspersen and Pacala 2001; Vilà et al. 2007; Belote et al. 2011; Paquette and Messier 2011; Gamfeldt et al. 2013; Seidel et al. 2013; Vilà et al. 2013). Such studies can be affected by the covariation of the tree species number with variables like stand age, successional stage, and/or site variables (Vilà et al. 2005, 2007; Vallet and Perot 2011). However, studies on this topic based on experimental data are still scarce (Scherer-Lorenzen et al. 2007; Drössler et al. 2015). Moreover, Whittaker (2010) addressed the scale dependence of the species richness–productivity relationship. Species evenness was found to explain forest productivity together with species richness in the global meta-analysis of Zhang et al. (2012). However, only a few other studies have analysed the influence of species evenness and richness on stand growth or productivity (Liang et al. 2007; Szwagrzyk and Gazda 2007; Lei et al. 2009).

Horizontal tree distribution pattern: spatial pattern and intermingling

Horizontal spatial pattern

The horizontal spatial pattern of trees is an important attribute of stand structure, which provides an idea of the variation in tree spacing rather than stand density which represents its average (McElhinny et al. 2005). It directly influences many ecological processes in forest ecosystems, such as tree growth and stand productivity, stand stability, or regeneration capacity. Besides inter- and intra-specific competition and silvicultural activities, site conditions have the greatest influence on horizontal spatial pattern in mixed forests (Getzin et al. 2006). Thus, contrasting environmental conditions may cause feedbacks between spatial structure and demographics. The three main types of spatial pattern regularity can be defined as: (1) regular; (2) random (Poisson); and (3) clumped (aggregated) in varying degrees, depending, in natural forests, on site, species composition, sampling scale, and stand age (Szwagrzyk and Czerwczak 1993; Hanewinkel 2004; von Oheimb et al. 2005; Paluch 2007). There are different approaches to studying the spatial distribution of trees, with a large number of available methods and indices described in the literature (e.g. Dale 1999; Pretzsch 2009; Gadow et al. 2012).

Some approaches that use tree positions provide detailed information about patterns at different spatial scales (Ripley's K-function, L function, etc.). However, methods that provide an index or mean value for the stand are required for studies at stand level, such as the Clark and Evans aggregation index or Pielou's distribution index (Table 1). In this way they can be easily integrated into any analysis.

Indices based on distances give a good estimation of spatial pattern, but in some cases it is not possible to take tree positions. There are some indices such as the uniform angle index (contagion index) that only use angle measures among neighbours (Gadow et al. 2012, p. 44), but their advantage over distance-based methods in terms of measurement is questionable. Other indices are based on local densities measured in sample quadrants (Pretzsch 2009, pp. 252–255) (Table 1), which can be useful for studying seedling and sapling distribution.
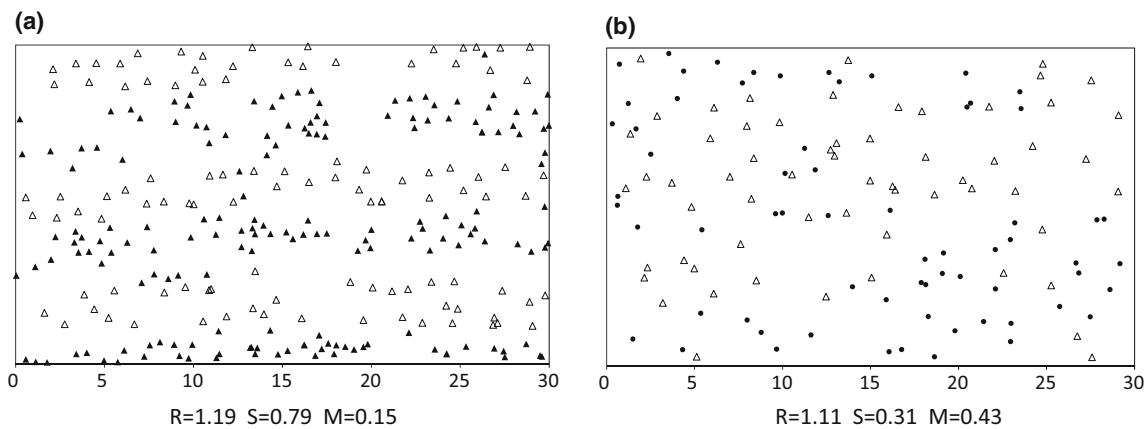
Species intermingling

The mingling pattern is the result of multilateral relationships of various factors influencing horizontal spatial distribution in mixed-species stands and varies from a tree-to-tree intermingled pattern to pronounced segregation. For a given species composition, the stand dynamics can differ substantially depending on the type of species intermingling, as this will determine whether intra- or inter-specific competition is the prevalent interaction between trees and, consequently, to what extent mixing effects can be expected (Pretzsch 2009, pp. 227–229). The first classification of mingling spatial patterns was presented by Langhammer (1971) who identified them as forms of mixtures and distinguished three main categories: tree-wise (tree-to-tree, intimate), row-wise, and group-wise patterns. Another classification is given from Pielou's segregation index (segregated, independent or random, and associated; Table 1).

To quantify species mingling, a number of indices were elaborated which allow comparative studies of different stands (Table 1). Most of these indices are based on the species intermingling proposed by Gadow (1993), which quantifies the proportion of neighbours of another species, providing a tree value that can be averaged at both species and stand level (Fig. 1). The mean value of species intermingling can be compared to the expected mingling (Lewandowski and Pommerening 1997). The spatial diversity status combines this index with the species richness, which gives the species average spatial status when averaged by species and the tree species spatial diversity when averaged by stand (Gadow et al. 2012, pp 57–62).

Several studies have highlighted the influence of horizontal spatial distribution and species mingling on stand growth in mixtures using individual tree modelling approaches (Pretzsch 1995a; Ngo Bieng et al. 2013; Rötzer 2013). However, scarce research based on empirical data has been conducted into these effects at stand level. Pretzsch et al. (2012a) compared the stand growth in pure and mixed stands with two intermingling patterns in mixed plots, finding overyielding or higher productivity in mixed stands only when there was a tree-wise pattern.

Fig. 1 Quantification of the horizontal tree spatial pattern (R) and species intermingling (S and M; see Table 1) in long-term experimental plots: **a** even-aged, row-wise mixed stand of *Pinus pinaster* Ait. (*open triangle*) and *Quercus pyrenaica* Willd. (*filled triangle*) stand in Lubia (Spain); **b** even-aged, tree-wise mixed stand of *Fagus silvatica* L. (*filled circle*) and *Pinus sylvestris* L. (*open triangle*) in Vallejimeno (Spain)

Vertical tree distribution pattern

The vertical stand structure in mixed stands is characterized by the spatial arrangement of different tree species in a forest stand along the vertical axis. Vertical structure affects the main processes in forest stand dynamics, modifying the supply, capture, and efficiency of use of resources and therefore the intra- and inter-specific interactions. It is also closely related to stand resilience against abiotic disturbances. According to Leikola (1999), who adopted Langhammer's (1971) classification, mixed forests in the strictest sense comprise trees belonging to the same storey. However, mixed-species stands are often stratified in height by species due to differences in height growth patterns, top height limits, and shade tolerance characteristics (Larson 1992; Peterken 1996; Schütz 1999; see "Species-specific height growth and canopy space partitioning" section). In mixed stands composed of two vertical stories, described as stratified mixtures by Smith (1986, pp 488–511), one element of the stand (the understorey) might depend functionally on another element (the overstorey) and can fulfil different functions simultaneously, e.g. tending overstorey or understorey, additional timber production, or soil protection.

The traditional approach to presenting the vertical distribution pattern of tree species is to use a hand drawing of the vertical stand profile or a photograph, as has been frequently done in the case of primeval forests (Faliński 1986; Peterken 1996). However, a more advanced and complete description of vertical structure requires the spatial positions of trees to be specified along with their size and species. Tree height is a particularly important size variable which can be used to describe the vertical structure of the stand (Temesgen and Gadow 2004; McElhinny et al.

2005). If all tree heights are known or can be reliably estimated for each species, frequency histograms can show the distribution of stem density, basal area, biomass, LAI, etc., for each tree species separately within defined height classes (Brokaw and Lent 1999; Parker and Brown 2000; Bongers 2001). Descriptive statistics of these height distributions might be used in stand-level analysis in the same way as diameter distributions (see "Mean tree size and tree size distributions" section). Similarly, mean height and standard deviation or variation coefficient of tree height can be used as a straightforward index to assess vertical structure (Barbeito et al. 2009). However, it is important to take into account that standard deviation might be underestimated when some tree heights are estimated instead of being measured.

The last potential approach involves using the distance-independent and distance-dependent structural indices (Table 1). Based on the principle of the non-spatial diversity index H by Shannon (1949), various authors have proposed specific measures to describe vertical differentiation in a forest stand. MacArthur and MacArthur (1961) calculated foliage height diversity, based on the proportion of leaf area within various height intervals above ground. As the determination of leaf area is very time-consuming, it is often replaced by the tree height diversity, based on the proportion of the trees in each height layer using the Shannon–Weaver formula (Kuuluvainen et al. 1996). Pretzsch (1995b) proposed the differentiation of tree species within each layer (Fig. 2) and the renaming of the index as species profile index (A). The standardized species profile index (A_{rel}) standardizes the species profile index, taking into account the number of species and the number of considered layers (Pretzsch 2009, pp. 282–283). This index has the advantage that it does not require information
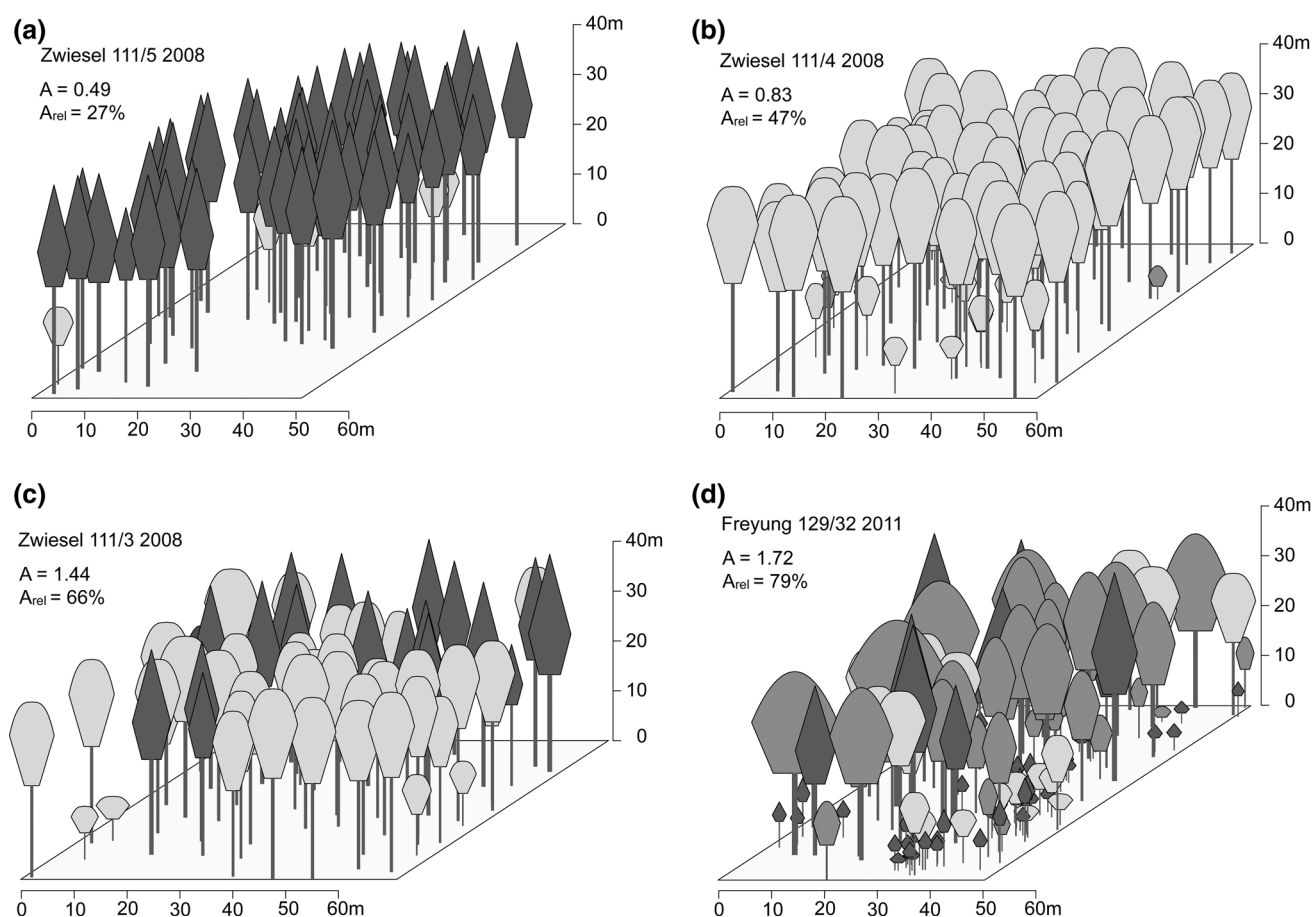
Fig. 2 Quantification of the vertical stand structuring on long-term experimental plots near Zwiesel and Freyung (Germany) by the species profile index (A) and standardized species profile index (A_{rel}) (Pretzsch 2009, pp. 281–283): **a** even-aged, mono-layered Norway spruce (*Picea abies* (L.) Karst) stand; **b** even-aged, mono-layered European beech (*Fagus sylvatica* L.); **c** even-aged mixed stand of Norway spruce and European beech; and **d** uneven-aged, multi-layered selection forest of Norway spruce, silver fir (*Abies alba* Mill.), and European beech

about the horizontal distribution while providing information about species vertical distribution. Staudhammer and LeMay (2001) proposed the use of basal area instead of tree numbers for calculating the proportion of species corresponding to each layer. Two spatially dependent structural indices that can also be used to assess vertical differentiation are the height differentiation index (Gadow 1993) and the structural complexity index proposed by Zenner and Hibbs (2000, Zenner et al. (2015).

Some studies have explored height growth patterns in mixed stands (Assmann 1953), but very few have included the analysis of vertical structure in mixed versus pure comparisons (Menalled et al. 1998) or in diversity–productivity relationships (Edgar and Burk 2001; Lei et al. 2009). As for the horizontal spatial pattern of trees, some competition indices include the effect of the vertical distribution of crowns (Biging and Dobbertin 1992; Pretzsch et al. 2002), but an analysis of the effect of species vertical distribution at stand level is lacking.

Mean tree size and tree size distributions

The tree size distribution in a forest stand can be understood as a property that emerges from the demographics of individuals, and therefore represents an intermediate scale between tree and stand level. The simplest way to describe a mixed forest for a given point in time is through the use of stand tables displaying the number of trees, basal area or volume per species, and diameter classes. Although approaches based on diameter classes have some inherent weaknesses, they provide useful information about stand structure for modelling and understanding forest dynamics in the long run. However, in order to use this information at stand level, the size distributions have to be described according to attributes at this level.

Basic statistics of distributions such as minimum, mean, maximum, standard deviation, skewness, or kurtosis have been used to study the effect of mixing on size distribution dynamics (Pretzsch and Schütze 2014, 2015). Information

concerning the number and the size or the respective mean size for each of the existing species should be presented separately. An overall value can be easily calculated as a weighted mean according to the proportions of the species. This method takes into account the species-specific mean tree size as well as their occupancy, but depends on the definition of species proportion (see "Species composition: species proportion, species richness, diversity and evenness" section).

The most common approaches to describe stand size distributions include the use of a diameter distribution model based on probability density functions (e.g. the Weibull or Johnson's SB functions) for each species. The diameter frequency data of mixed-species stands, unlike pure stands, may have highly irregular shapes, including multi-modes. So, the use of uni-modal statistical distributions when attempting to apply distribution models can lead to oversimplified descriptions of stand structure. One option to avoid this limitation is the use of a "mixture" distribution or finite mixture model (FMM), which considers a frequency distribution made up of two or more component distributions. FMM was introduced by Liu et al. (2002) to characterize diameter distributions in mixed stands. The FMM models can provide a useful tool for effectively managing mixed-species stands, as these models are more flexible for describing highly skewed and irregular diameter distributions for the whole plot, while providing an acceptable estimation for each species component and the mix proportions (Liu et al. 2014; Podlaski and Roesch 2014; Pach and Podlaski 2015). Distribution-free methods have also been proposed to describe multi-modal distributions such as percentile prediction (Borders et al. 1987) or nonparametric statistical methods (Droessler and Burk 1989; Haara et al. 1997; Maltamo and Kangas 1998).

Other indices that describe size heterogeneity, such as the size differentiation index proposed by Füldner (1995), the Gini coefficient (de Camino 1976) or the Shannon index applied to tree sizes, have been employed to relate size heterogeneity to stand dynamics (Liang et al. 2007; Lei et al. 2009; Varga et al. 2005).

Age composition

When characterizing the structure of a mixed stand, age composition or age structure should also be taken into account. Frequently, the age structure is summarized in a single indicator of mean stand age, which implies the use of different definitions according to the requirements of each study (e.g. Garet et al. (2012) analysed the use of dominant age as an indicator of sustainability by measuring 4–9 randomly selected canopy-dominant or codominant trees but avoiding overdominant or overstory trees). As for monospecific stands, the terms even-aged,

two-aged, and uneven-aged are used to refer to the age composition.

Assigning an age to an even-aged mixed forest is not technically problematic and can be determined by coring individual trees. However, the number of cored trees per species required to estimate stand age can vary greatly among studies (Chen et al. 2003; Lei et al. 2009; Waskiewicz et al. 2013). In uneven-aged stands, stand age is often replaced by the dominant age (Garet et al. 2012) or dominant age by species (Lee et al. 2004).

Due to the difficulties associated with age determination, diameter or related indices are often used as a surrogate for age. The most common index is the number of large trees, sometimes called number of old-growth trees (Barbati et al. 2012), by using a threshold diameter to define large trees ranging from dbh > 65 cm to dbh > 100 cm (McElhinny et al. 2005) or specifying a threshold by species (Alberdi et al. 2013). Despite the difficulty and expense of age structure estimation in mixed stands, it is important to consider this stand characteristic as it is related to stand productivity (showing different patterns in mixed forest for a variety of age structures; e.g. Binkley and Greene 1983, Waskiewicz et al. 2013) and forest dynamics (e.g. Coomes and Allen 2007).

Characterization of the dynamics of mixed-species forest stands

Mixed stands, which depend on both intra-specific and inter-specific interactions, often do not perform in exactly the same way as the weighted mean of the respective pure stands, but rather show a differential behaviour due to the presence of mixing effects (Pretzsch and Schütze 2009). The interactions may strongly modify the trajectories on which the associated species proceed. However, the outcome of the species interaction depends on the ecological traits of the species and on the environmental conditions.

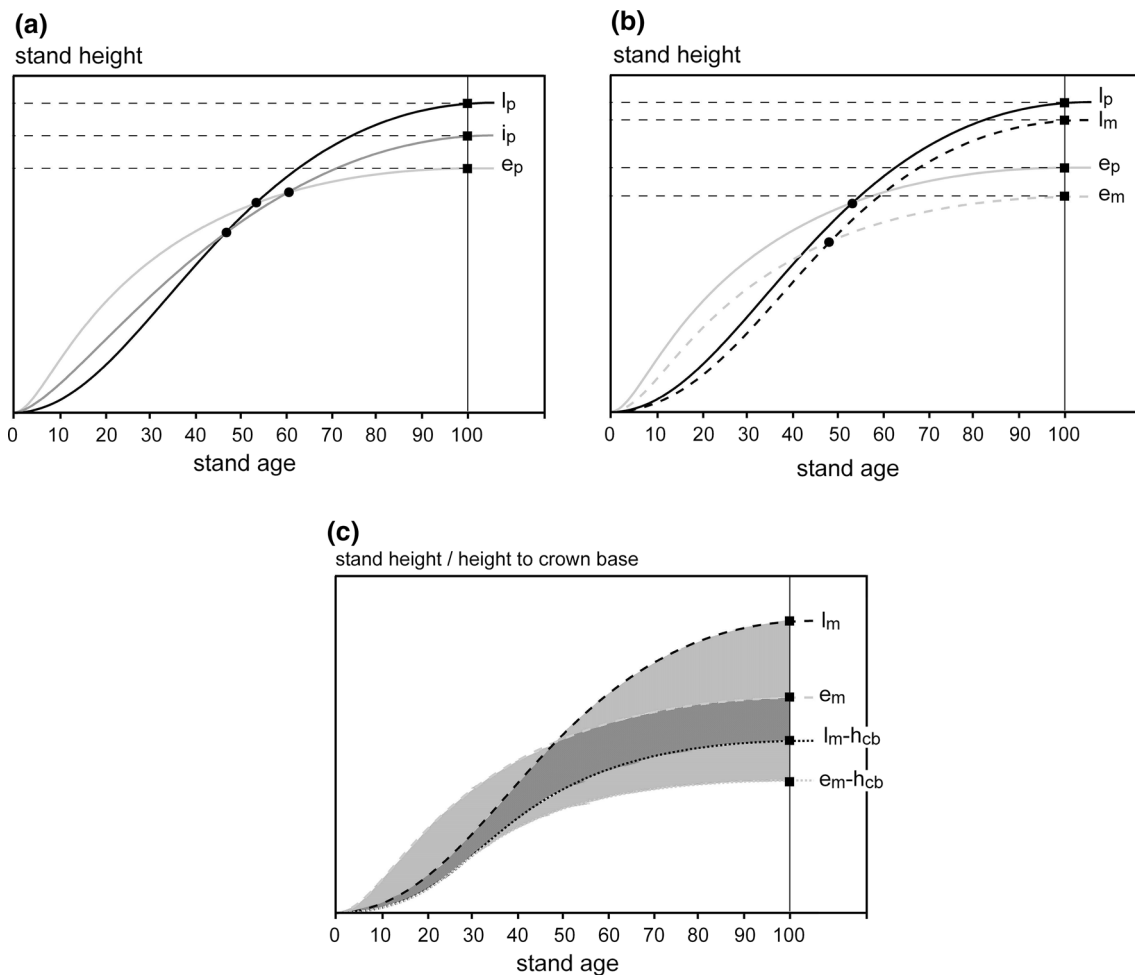### Species-specific height growth and canopy space partitioning

As the height development of a forest stand is linked to many other stand attributes, it is commonly used for characterising the species-specific dynamics of pure stands (Skovsgaard and Vanclay 2008). The height growth curves are species specific, with distinct differences in the sigmoid height growth curve of early-successional and light demanding (e.g. *Betula*, *Larix*, *Pinus*), late-successional and shade tolerant (e.g. *Abies*, *Fagus*, *Picea*), as well as intermediary species (e.g. *Acer*, *Tilia*, *Fraxinus*; Assmann 1970, pp. 44–45). The species-specific levels of the height curves in monospecific stands and the age of intersection

reveal the height and light competition to be expected when tree species are mixed (Fig. 3a). They point to ways in which competition can be released by temporal (planting or natural regeneration in advance in order to achieve age difference) or spatial (groups in order to obtain intra- in addition to inter-specific competition) separation of the species.

While in pure even-aged stands, intra-specific competition only has a minor effect on the mean height development and is negligible for the top height, inter-specific competition can considerably modify species-specific growth patterns, especially when species with very different height curves are mixed. Figure 3b shows the common slowing down of the height growth of mixed-species (Wiedemann 1951, pp. 131–133). However, these changes in species-specific height growth curves in mixed stands can vary significantly with stand

density (Amoroso and Turnblom 2006; Garber and Maguire 2004).

The vertical distribution of tree species might change over the stand development through tree growth and regular mortality, besides the effect of natural disturbances and human operations (Latham et al. 1998; Oliver et al. 1999). The leading species commonly reduces the growth of the lower species by pre-empting the light, while the lower species may reduce the growth of the leading ones by using water and mineral nutrients which are not sufficient for all the trees and by entering and reducing their crown space from below (Knapp 1991; double hatched area in Fig. 3c). Differences in tree ages and microsites in the stand can be a major factor in either the maintenance of or shift in height dominance between species and the vertical stratification (Larson 1992; Kelty 1992). The point of intersection of the height curves of the two species in the mixture indicates the stand age at which

Fig. 3 Course of species-specific height and height to crown base provides key information about the dynamics of mixed-species stands. Schematic representation of **a** sigmoid height growth in pure stands (p) for early-successional (e_p), intermediate (i_p), and late-successional tree species (l_p); **b** slowing down of height growth for early- (e_m) and late-successional (l_m) by inter-specific competition in mixed-species stands; and **c** ingrowth of the late-successional and shade tolerant species in the mixed stand (l_m) into the crown layer of the early-successional fast-grower (e_m). H_{cb} height to the crown base

the previously suppressed species might take the lead (Fig. 3b). Therefore, the ratio of mean heights between species at a given stage is a simple and effective indicator for considering species stratification over the stand development in a stand-level analysis (Edgar and Burk 2001) (Table 2).
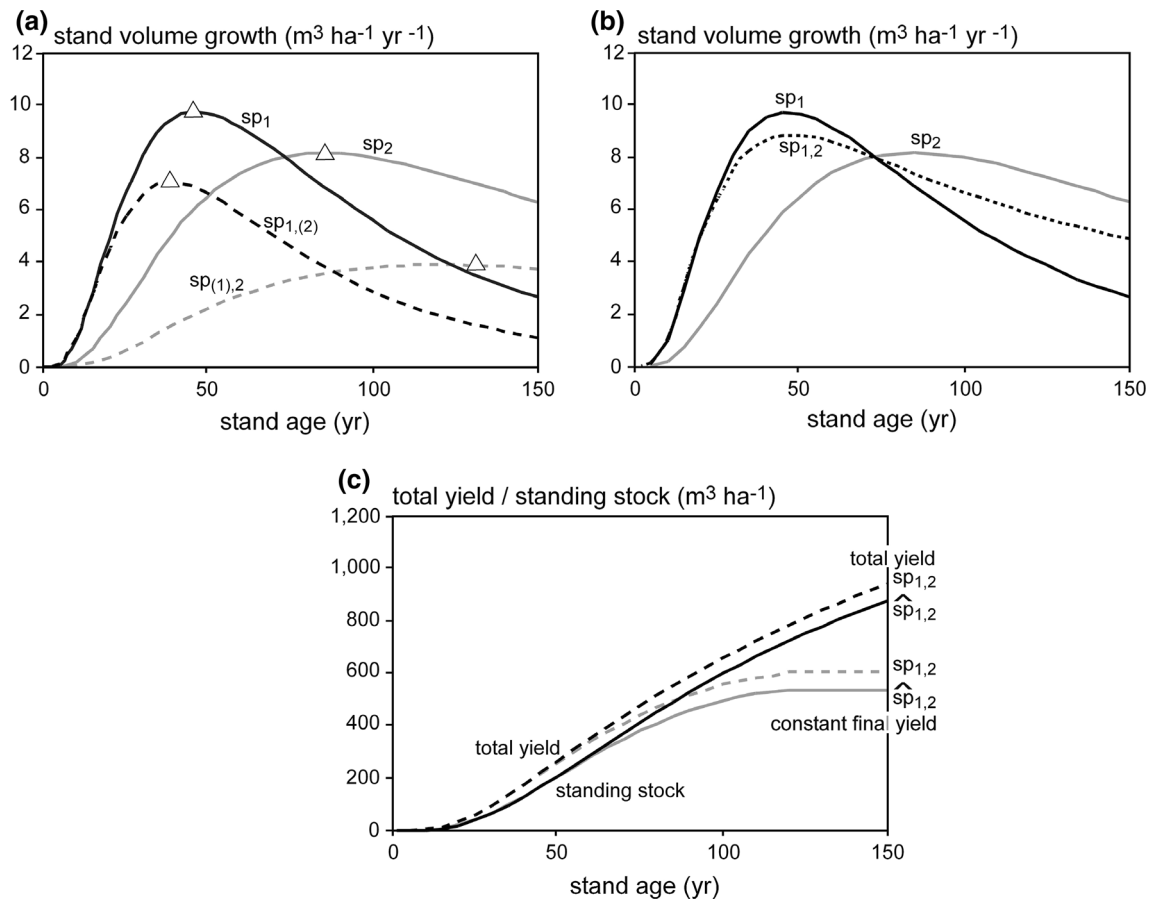
Course of growth, yield, and standing stock at tree species and stand level

As with height growth, the species-specific level and rhythm of the course of annual volume growth can be

Table 2 Indices for characterizing the dynamic at stand level in mixed-species stands

Dynamic aspect	Concept	Measure	Pros (+) and cons (−)	References
Height growth and canopy space partitioning Volume growth and yield	Influence of species-specific height growth patterns on canopy space partitioning dynamic (Fig. 3)	Height curves ($H_i = f(t)$) Age at intersection of species height curves Ratio between species mean heights (H_1/H_2)	+Mean height by species easily measured +Easily interpreted −Need long-term measurements −Dependent on stand density and mixture composition	Wiedemann (1951) Kelty (1992) Oliver and Larson (1996) Edgar and Burk (2001)
	Changes of species-specific volume growth patterns in mixed stands (Fig. 4)	Mean annual increments by species and total (MAI_i, MAI) Current annual increments by species and total (CAI_i, CAI)	+Frequently used in forest practice −Need long-term measurements −Dependent on stand density and mixture composition	Mitscherlich (1970)
	Standing stock and total yield developments	Standing stock curve ($V = f(t)$) Total yield curve ($VT = f(t)$) Constant final yield CFY	+Easily interpreted +Linked to stand productivity −Need long-term measurements −Dependent on stand density and mixture composition	Mitscherlich (1970) Weiner and Freckleton (2010)
Self- and alien-thinning	Density reduction along age	Mortality rates by species and total	+Easily interpreted −Need long-term measurements −Dependent on stand density and mixture composition –Not illustrative of the self-thinning trajectory	
	Self- and alien-thinning trajectories (Fig. 5)	Intercept of size–density relationship by species and total Slope of size–density relationship by species and total (α_i, α) Mean tree size at which CFY is reached	+Reflection of the trajectories +Linked to stand productivity −Need long-term measurements −Dependent on mixture composition	Reineke (1933) Pretzsch et al. (2012a, b)
	Maximum stand density is the boundary of self- and alien-thinning line	Maximum stand density index (SDI_{max}) Maximum basal area at a given dominant height (BA_{max})	+Easily interpreted +Linked to stand productivity −Dependent on mixture composition and structure −Not illustrative of the self-thinning trajectory	Sterba (1987) Puettmann et al. (1992) Sterba and Monserud (1993) Woodall et al. (2005)
Growth partitioning among trees	How much volume of trees of different sizes contribute to the total stand volume growth (Fig. 6)	Growth dominance coefficient (GDC)	+Easily interpreted −Need volume and volume growth of all trees −Dependent on stand stage development	Binkley et al. (2006)
	Relationship between tree growth and tree size	Growth–size relationship	+Less data requirement −Dependent on site, density, age	Weiner (1990) Pretzsch and Schütze (2014)

Fig. 4 Mixing can modulate the course of stand growth, yield, and standing stock: **a** course of annual volume growth in pure stands (sp$_1$ and sp$_2$) and of both species in a mixed stand (sp$_{1,(2)}$ and sp$_{(1),2}$; see notation in Table 4); *triangle* the level and the age of culmination; **b** the course of total stand growth in mixed (sp$_{1,2}$) compared with pure stands (sp$_1$ and sp$_2$); **c** the course of the total yield (*black lines*) and the constant final yield (end of *grey lines*) higher in mixed (sp$_{1,2}$) compared with the weighted mean of pure stands ($\hat{sp}_{1,2}$). Notice that this example assumes positive mixing effects

modulated in mixed-species stands (Mitscherlich 1970, pp 112–126; Pretzsch et al. 2015b). The changes in species-specific growth patterns result in a total mixed stand growth curve that can differ significantly from those curves in pure stands. Figure 4a shows an example of two species with different growth trajectories in pure stands. The growth rhythms of species 1 and 2 differ even more in mixed stand due to the anticipation and postponing of the growth rhythms of species 1 and 2, respectively. The growth can continue longer at a relatively high level and decrease both later and more slowly in mixed versus pure stands (Fig. 4b). Thus, the total yield of the mixed stand can be higher than that of weighted mean of the pure stands (Fig. 4c, upper curves). The mixed stand may have a higher standing stock and constant final yield compared with the weighted mean of both pure stands due to a higher supply, capture, or resource use efficiency. By the constant final yield we mean the maximum level of standing stock a stand at a given site can achieve before senescent-related

mortality reduces the standing stock beneath this maximum level (Oliver and Larson 1996, pp. 340–343).

The modification of volume growth and yield by tree species mixing can be characterized and quantified by the two approaches summarized in the second section on Table 2. First, the trajectories of mean annual increment and current annual increment at the species and total stand level in mixed compared with pure stands are informative. Key characteristics of these trajectories are the levels and the points in time of the culmination. Second, the development of the standing stock and total yield in mixed compared with pure stands reveals changes in yield and carrying capacity. Standing stock and total yield at given points in time may be used as key characteristics. Of special interest may be changes in the level of constant final yield (Weiner and Freckleton 2010) due to niche complementarity and higher packing density in mixed stands. Mixing may enable from the initial to the final stand development phase a 10–20 % higher

maximum stand density compared with neighbouring pure stands.

Self-thinning and alien-thinning

Self-thinning is the result of competition between trees for resources and is usually expressed by the size–density relationship when there is maximum site occupancy. In forestry, the expression proposed by Reineke (1933) is the most frequently used ("Stand density" section). The self-thinning trajectory, expressed in a double logarithm scale as a line with slope α, includes an early open grown stage when stands remain relatively constant in tree number (Fig. 5a). When they become fully stocked and the trees start to deal with crowding, the size–density trajectory follows the self-thinning line or maximum stand density relationship (MSDR). The standing stock can increase until it reaches the constant final yield which is determined by the site conditions (Körner 2002; Oliver and Larson 1996). From this stage on, any increase in mean tree diameter or volume is accompanied by a proportional loss in tree number. Reineke (1933) reported a general value of -1.605 for the slope (α) of the MSDR, but there is evidence that it varies among species in pure stands (e.g. Pretzsch and Biber 2005; Charru et al. 2012), expressing the species' self-tolerance (Zeide 1985).

The self-thinning line might differ between mixed and pure stands as a consequence of differences in requirement, capture, and use efficiency of resources among species. Three main aspects of the size–density trajectories can be changed by species mixing (Pretzsch et al. 2012b). Firstly, the level of the stand self-thinning line may be shifted upwards (or downwards) as the packing density in an inter-specific neighbourhood might be higher than under intra-specific conditions. Secondly, as the species involved interact, the slopes of their size–density trajectories may deviate distinctly from that in pure stands, such that self-thinning turns into alien-thinning (i.e. density-dependent mortality caused by the inter-specific competition; Harper 1977, p. 171). Thirdly, the bending of the size–density trajectory may occur later (Fig. 5b), as the density level can be higher in mixed compared with pure stands and the stands may fall later beneath the maximum level. The causes for the increased level may be a higher carrying capacity due to niche complementarity. The reason for the later bending beneath the maximum density level may be higher diversity in tree sizes and ages which enable a longer-lasting stand closure and delay of the senescent-related mortality and opening up of stands in the mature development phase. Suitable measures for describing latter aspects of mixed compared with pure stands are the level of the total stand self-thinning line and the slopes of the self-thinning lines of the stand as a whole and each species separately. Of additional interest may be the stand age at which the constant final yield is achieved, i.e. the self-thinning line is bending towards a slope of $\alpha = -2.0$ (Fig. 5b).

As presented in "Characterization of mixed stands structure" section, the assessment of density and mean tree size in mixed stands is hampered by methodological difficulties. Data from temporary plots (forest inventory data) have been used for estimating maximum density in mixed stands (Woodall et al. 2005). However, data from permanent plots from fully stocked and unthinned stands are typically needed to estimate the self-/alien-thinning line and to improve our understanding of the size–density dynamic in mixed stands, research in this area still being somewhat scarce (e.g. Puettmann et al. 1992; Poage et al.
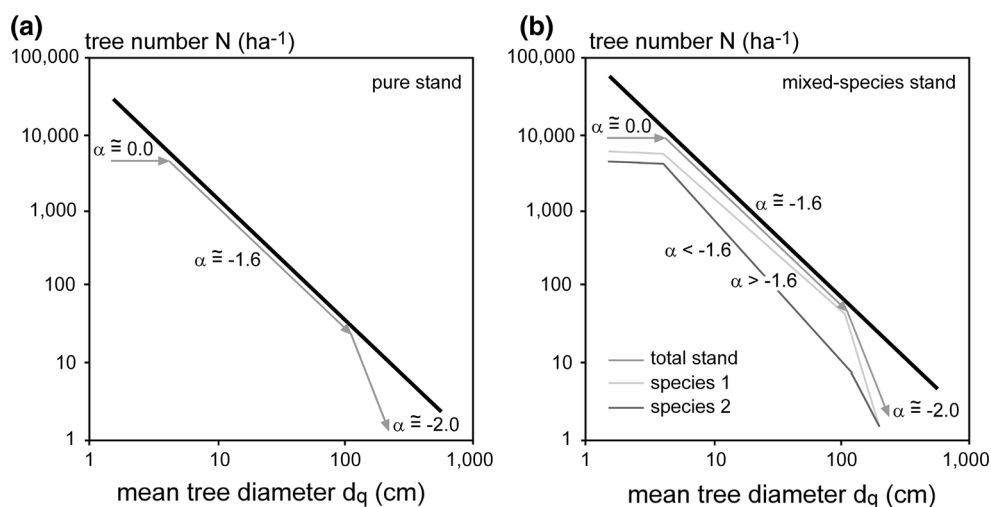
Fig. 5 Decrease in tree number (N) per unit area over mean tree size (d_q) in double logarithm scale, and the respective slopes (α), caused by **a** self-thinning in pure stands and **b** combined self- and alien-thinning in mixed-species stands in schematic representation. The point of change from $\alpha = -1.6$ to $\alpha = -2$ indicates the moment at which constant final yield is achieved

2007; Reyes-Hernandez et al. 2013). Estimating maximum densities using alternative statistical techniques, such as quantile regression or stochastic frontier analysis, may mitigate this challenge (Zhang et al. 2005, Vospernik and Sterba 2014), but applications to mixed-species stands have been rare (Ducey and Knapp 2010).

Studies of the MSDR in mixed stands have been conducted by adapting/modifying the MSDR methods employed in pure stands. There are two general methods which are: combining species components and separating species composition. Early results showed that by combining data for all species in a stand, the intercept and slope had values similar to those in pure stands (Weller 1987). Separation of species has been done by means of purity of primary species (Weiskittel et al. 2009) or by applying the summation method by species (Woodall et al. 2005).

In some studies a maximum density surface instead of a line is described to account for changes in species proportion so that the intercept and the slope can vary depending on the mixture (Sterba 1991; Puettmann et al. 1992) and the structure of the diameter distribution (Sterba and Monserud 1993; Gül et al. 2005). However, calibrating these surfaces for multiple or complex mixtures would require huge data sets. Woodall et al. (2005) proposed a generalization of self-thinning lines using the specific gravity functional trait to go beyond the species identity by extending the negative linear relationship between maximum SDI and specific gravity (Dean and Baldwin 1996). In that case, the maximum SDI can be a function of the mean specific gravity of the species in the mixed stand.

## Growth partitioning among trees of different size

A crucial characteristic of stand dynamics, strongly determined by stand structure, is the fact that stand growth involves trees of different sizes. The growth partitioning among trees of different size is linked to the mode of competition, i.e. the degree of size asymmetry. According to Weiner (1990), competition for light is mainly size asymmetric while competition for below-ground resources is generally size symmetric, and therefore the site conditions influence the degree of size asymmetry (Pretzsch and Biber 2010). In pure stands, growth partitioning among the trees of different sizes is often size asymmetric, as the tallest trees in fully stocked middle-aged stands can pre-empt light and grow over-proportionally due to their superior height and therefore greater access to light (Schwinning and Weiner 1998; Hara 1992, 1993). As mixing can modify above-ground and below-ground resource use, it can have an important effect on the distribution of growth between the trees in a stand and therefore on the mode of competition (Hara 1992, 1993; Pretzsch and Schütze 2014, 2015; Río et al. 2014).

The way in which the growth in a stand is distributed among trees of different sizes can be characterized by the relationship between the cumulative tree volume growth and cumulative tree volume (Binkley 2004; Binkley et al. 2006). The resulting curve illustrates how much small trees contribute to the total stand growth compared with tall trees (Fig. 6a). Mixing may modify the growth distribution among trees of different sizes due to more equal growth efficiency of dominant and understorey trees (Fig. 6b).

Beyond the graphical representation, the course of the curve can be characterized by the difference in the Gini coefficients for cumulative growth and the Gini coefficients for cumulative volume, which is equivalent to the growth dominance coefficient (GDC) used by Binkley et al. (2006). This coefficient is zero (GDC = 0) when all trees contribute to stand growth proportionally to their volume (bisectoral line in Fig. 6a), GDC > 0 when there is a

Fig. 6 Schematic representation of the cumulative distribution of tree volume growth (ordinate) over cumulative tree volume (abscissa) for forest stands with different competitive status of small compared with tall trees: **a** the curves 1, 2, and 3 represent, respectively, stands with low, medium, and strong contribution of small trees to the total stand growth; **b** the curves for mixed stands may approach the bisector line (size symmetric) compared with pure stands
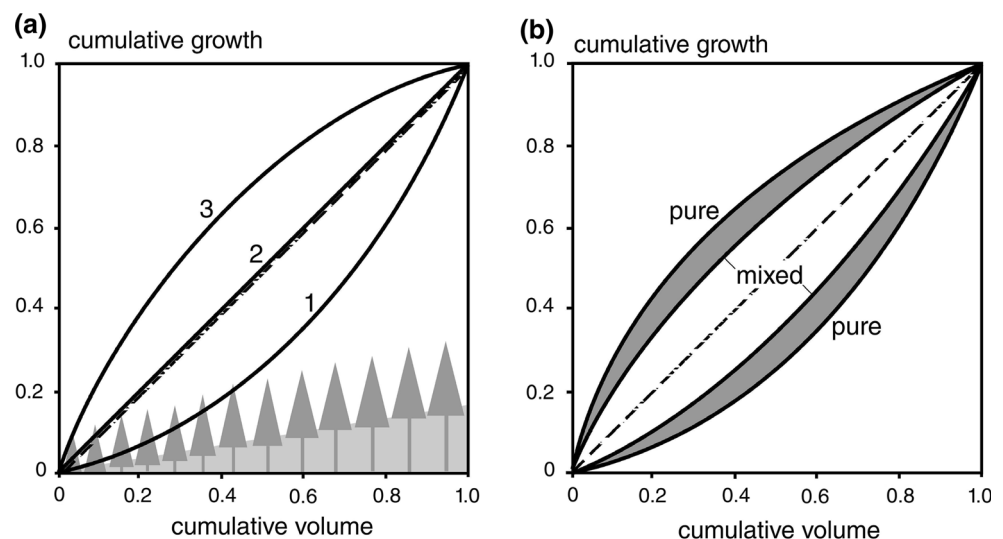
growth dominance of tall trees, and GDC < 0 when there is a growth dominance of small trees (Fig. 6a—curves 1 and 3, respectively). For mixed stands, Katholnig (2012) found that in the average even-aged and uneven-aged mixed-species stands the GDC was negative, while it was positive for pure stands.

The mode of competition can be directly analysed through the direct exploration of size growth-size relationships (Weiner 1990; Pretzsch and Biber 2010), which can be also employed to compare the mode of competition in mixed versus pure stands (Pretzsch and Schütze 2014, 2015).

Productivity of mixed-species stands

Stand site productivity indices

The term site refers to a geographic location that is considered homogeneous in terms of its physical and biological environment (Skovsgaard and Vanclay 2008). From a management point of view the productivity of a site is based upon the net stem growth harvested during the rotation period, which represents about 30 % of net primary productivity in lightly thinned stands if mortality and thinned trees are taken into account (Pretzsch 2009, p. 80). The most common way to estimate site productivity in forestry is by constructing site productivity indices based on three fundamentals (Skovsgaard and Vanclay 2008): (1) site classification by stand height, (2) Eichhorn's rule describing the relationship between total growth and stand height, and (3) the thinning response hypothesis. Other approaches to classifying forests according to their potential productivity are based on processes or direct productivity–environment relationships (Bontemps and Bouriaud 2013).

For even-aged forest stands, the most widely used site productivity index is the site index (SI), defined as the dominant height of a stand at a reference age. It is an indicator of forest site productivity which becomes very indicative when coupled with a volume production indication by Eichhorn's rule (Skovsgaard and Vanclay 2008). Dominant height has the advantage that it is hardly influenced by stand management measures such as thinning (Assmann 1970), although it can be modified by low (Weiskittel et al. 2009) or high stand densities (MacFarlane et al. 2000; Ritchie et al. 2012). Its importance in pure stands is demonstrated by the myriad of study cases that use it to classify stands according to their timber productivity or in forest growth models (Burkhart and Tomé 2012 and references therein). However, its applicability to mixed forests is unclear for two main reasons: (1) Eichhorn's rule in mixed stands is questionable since the relationship between total yield and dominant height can deviate from that expected for mono-specific stands due to inter-specific interactions; (2) the two variables needed to determine SI are difficult to assess in mixed stands.

In order to estimate the dominant height in mixed stands tree species identities must not be considered when selecting dominant trees (Zingg 1994). Thus, among this population the mean height by species can be calculated. The other option would be to calculate the dominant heights by species considering the area occupied by each species (Keller 1995). However, for a given site and age these dominant heights will depend on species proportion (Sterba 1996) as the dominant height growth of tree species can differ from that of the same species in a pure stand (Pinto et al. 2008).

Despite the limitations of SI, the concept is so deep-rooted in our understanding of forest growth that it is still used in mixed forests (Table 3). Some examples are the site index conversion equations where the SI of one species is estimated from the SI of a second species growing in a mixed stand (Vospernik and Sterba 2001; Nigh 2002), the SI of the predominant species under investigation (Edgar and Burk 2001; Hein and Dhôte 2006), the same SI equation for congenerous species (Eriksson et al. 1997), the SI for each of the component species (Bollandsas et al. 2008), or the SI of one dominant species using parameter estimates of a full model fitted to all species in the mixture (Waskiewicz et al. 2013).

Estimating site productivity in irregular structures is complicated by variations in stand density, structure, composition in mixed stands, and suppression of subordinate trees (Berrill and O'Hara 2014). SI has been substituted in forest growth models of mixed or uneven-aged stands by using instead a past growth index (Trasobares et al. 2004b; Palahí et al. 2008) and actual site variables (Trasobares et al. 2004a) or by applying an age-independent site index approach (Tomé et al. 2006). The specific height attained at a reference diameter based on the allometric height–diameter relationship has also been proposed as a productivity index in southern uneven-aged and boreal mixed forests (Vanclay and Henry 1988; Huang and Titus 1993). Vanclay (1992) proposed a growth index for complex mixed tropical forests based on the diameter increment adjusted for tree size (diameter) and competition. He also suggested that periodic annual volume increment might indicate the site productivity, especially in unmanaged stands.

Other studies have avoided the use of site index in mixed forests by including site environmental variables in models (Vallet and Perot 2011; Adame et al. 2014; Toïgo et al. 2015). This method is promising as a way to account for site productivity, as environmental variables at larger scales are becoming increasingly available.

Table 3 Indices for characterizing the productivity in mixed-species stands

Productivity variable	Concept	Measure	Pros (+) and cons (−)	References
Site productivity indices	Net primary production during the rotation period	Net primary productivity (NPP)	+Direct measure of productivity −Difficulty and costly estimated −Need long-term data	
	Dominant height at a reference age is correlated to total yield in even-aged stands	Site index (SI) Site index conversion equations	+Frequently used in forest practice −Dependence on mixture composition −Eichorn's rule not tested in mixed stands −Not valid for uneven-aged stands	Eriksson et al. (1997) Nigh (2002) Skovsgaard and Vanclay (2008)
	Allometric height–diameter relationships in uneven-aged stands	Height at a reference diameter	+Easily estimated −Influenced by density −Not adequate for even-aged stands	Vanclay and Henry (1988) Huan and Titus (1993)
	Productivity based on environmental variables of the site	Productivity–environment relationships	+Based on site characteristics −Need large data bases −Generally poor correlations	Bontemps and Bouriaud (2013)
Growth–density	The thinning response hypothesis: for a range of residual basal area stand volume growth does not decrease	Maximum, optimal, and critical basal areas	+Based on common stand variables −Need comparable stands with different densities −Dependent on site, age, and mixture composition	Assmann (1970) Zeide (2001)

## Growth–density relationships interacting with species mixture effects

In the case of pure stands, it is well known that the higher the density, the higher the productive potential and the greater the stand productivity. Beyond a threshold density, stand productivity no longer depends on density. This growth–density pattern is expressed by Wiedemann's hypothesis (Assmann 1970, pp. 229–235) or Langsaeter's plateau (Langsaeter 1941), also known as the thinning response hypothesis (Skovsgaard and Vanclay 2008). In most cases there is an optimum density at which growth is maximum and somewhat higher than the growth at maximum density. Depending on the species, age, and site quality of the pure stands, the optimum density may be more or less pronounced (Assmann 1970, pp. 253–258; Kennel 1972; Pretzsch 2005).

As regards mixed stands, research in this area has been largely neglected because of the lack of suitable data (Pretzsch 2003). Due to the presence of interspecific interactions, the growth–density relationships in mixed stands will most probably be different from those generally observed in monospecific stands. There are several issues that should be taken into account when analysing the growth–density relationships of mixed stands in comparison with monospecific stands: (1) the greater difficulty to define relative density in mixed stands ("Stand density" section); (2) the variation in species proportions that may occur in mixed stands; (3) the greater absolute density that may be found in mixed stands (Pretzsch et al. 2015b); and (4) the possible interaction of the mixing effects with density (Garber and Maguire 2004; Amoroso and Turnblom 2006; Condés et al. 2013). Therefore, the complexity of species interactions, influenced by species composition, stand characteristics, and site factors makes it difficult to establish and test a general hypothesis for the growth–density relationship in mixed stands.

Pretzsch (2002) hypothesized that through the better use of niches by different species in the same stand, there will be no such optimum, and maximum growth can be maintained over a wider range of densities (Fig. 7), which does not necessarily mean greater productivity in mixed forests, but a greater resilience to disturbances, especially if risk is considered in the analysis (Pretzsch 2005). This hypothesis was corroborated by the findings of del Río and Sterba (2009) and Huber et al. (2014), where a quadratic term in the growth–density relationship for mixed stands was found not to be significant.
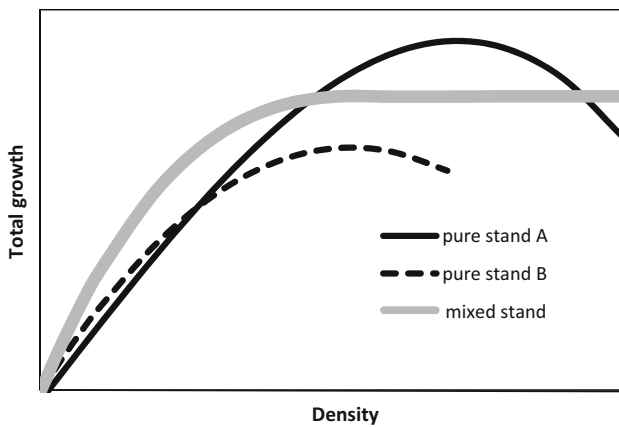
Fig. 7 Density–growth relationships in pure and mixed-species stands, modified after Pretzsch ([2002]). Both monospecific stands exhibit an optimum density, where total growth is maximum. The mixed stand of both species does not show an optimum density and—in this example—has a maximum growth between the two pure stands. Depending on at which density the stands are compared, the mixed stand will show transgressive overyielding (at lower densities) or not

To characterize these relationships, Assmann's ([1970], pp. 229–235) maximum, optimal, and critical basal areas can be used in the same way as for pure stands, but with the added difficulty of quantifying the influence which species proportion has on them (Table [3]).

Comparison of productivity in mixed versus monospecific stands on tree species and stand level

Many studies have found that mixing forest species results in over- or underyielding in comparison with monospecific stands due to interactions between species (Toïgo et al. [2015]). For many reasons, foresters may not only be interested in how the total growth of all species in a mixed stand as a whole compared to the growth in monospecific stands, but also in the behaviour of individual species in the mixture, compared with their growth in the respective monospecific stands.

The different species in mixed stands may show differences in growth habit, specific wood gravity, and species-specific growth rates that may impede the use of volume as a direct measure of site productivity (Vanclay [1994]). As a consequence, total biomass or biomass growth would appear to be the best alternative when comparing the production of mixed versus pure stands (Pretzsch et al. [2013]). However, due to the lack of species-specific knowledge, using total volume or volume growth is often the most realistic option.

In order to determine whether mixing affects productivity for a given species (i), the observed productivity (i.e. growth or total volume or biomass) of this species in a mixed stand
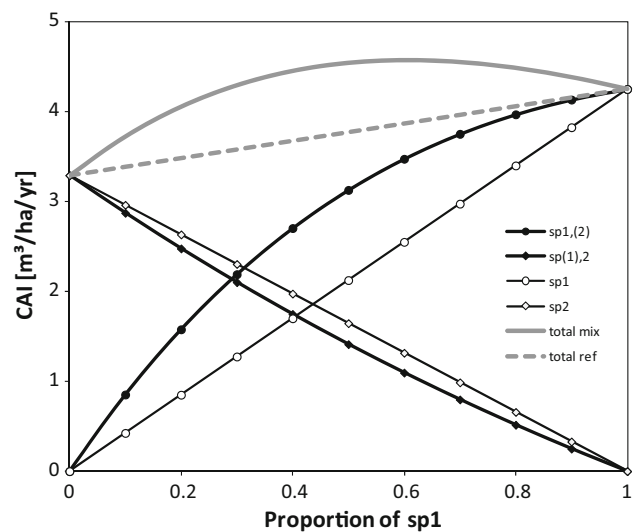
Fig. 8 Schematic representation of mixing effects by cross diagrams according to Harper ([1977]). In this example, species 1 has a higher current annual increment (CAI) in the pure stands (species proportion $= 1$) than species 2 (CAI when proportion of species 1 is 0). In the mixed stand, species 1 exhibits a positive mixing effect ($\mathrm{sp}_{1,(2)}$), i.e. it has a better growth than its reference. Species 2 exhibits a minor negative mixing effect ($\mathrm{sp}_{(1),2}$). Both species together have a positive mixing effect, not only having a higher increment than the reference, but even exhibiting a transgressive overyielding, because its increment is higher than the pure stand of this better growing species between a species proportion of species 1 of 0.25 and 1

($P_{i,\mathrm{mix}}$) is compared to the reference productivity of the species ($P_{i,\mathrm{ref}}$), assuming the hypothesis that there is no mixing effect ($P_{i,\mathrm{ref}} = P_i \cdot m_i$), i.e. the productivity of the species in a monospecific stand (P_i) times its proportion in the mixed stand (m_i). The observed productivity for the total mixed stand ($P_{\mathrm{mix}} = \sum P_{i,\mathrm{mix}}$) can be compared to the sum of the reference productivities of all the species in the mixture ($P_{\mathrm{ref}} = \sum P_i \cdot m_i$). If the observed productivity is higher than the reference productivity ($P_{\mathrm{mix}} > P_{\mathrm{ref}}$), this evidences a positive mixing effect (overyielding), whereas the opposite is true (underyielding) if the observed productivity is lower ($P_{\mathrm{mix}} < P_{\mathrm{ref}}$). It is particularly interesting when there is transgressive overyielding, i.e. the productivity of the mixed stand exceeds the productivity of the respective pure stands ($P_{\mathrm{mix}} > \max\{P_1, \ldots, P_i, \ldots P_n\}$). Analogously, degressive underyielding occurs when the productivity in mixed stands is lower than the respective productivity in pure stands ($P_{\mathrm{mix}} < \min\{P_1, \ldots, P_i, \ldots P_n\}$). The graphical representation of these relationships for a two species mixture is often known as Kelty's ([1992]) replacement series or cross-species diagrams (Harper [1977]; Fig. [8]).

The comparison of productivity in mixed versus pure stands can also be given in relative terms by species as well as for the total stand (Pretzsch et al. [2010], [2013]; Bielak et al. [2014], [2015]), i.e. the relative productivity by species (RP_i) and the relative productivity for the total stand

Table 4 Measures for comparing productivity in mixed with pure stands. In order to simplify the presentation the measures are given for mixed stands composed only of two species (species 1 and species 2), following the nomenclature used by Pretzsch et al. (2013)

	Species 1	Species 2	Total
Basic productivity variables			
Pure stand	P_1	P_2	–
Mixed stand	$pp_{1,(2)}$	$pp_{(1),2}$	$P_{1,2} = pp_{1,(2)} + pp_{(1),2}$
Mixed stand up-scaled to hectare	$P_{1,(2)} = pp_{1,(2)}/m_1$	$P_{(1),2} = pp_{(1),2}/m_2$	–
Mixed stand reference	$P_1 \cdot m_1$	$P_2 \cdot m_2$	$\widehat{P}_{1,2} = P_1 \cdot m_1 + P_2 \cdot m_2$
Comparison measures			
Absolute over-/underyielding	–	–	$P_{1,2} - \widehat{P}_{1,2}$
Relative productivity	$RP_{1,(2)} = P_{1,(2)}/P_1$	$RP_{(1),2} = P_{(1),2}/P_2$	$RP_{1,2} = P_{1,2}/\widehat{P}_{1,2}$
Ratio of productivity	$RPP_{1,(2)} = pp_{1,(2)}/P_1$	$RPP_{(1),2} = pp_{(1),2}/P_2$	$RPP_{1,2} = RPP_{1,(2)} + RPP_{(1),2}$

P is the productivity referred to the hectare, pp is the contribution of species to the total productivity in mixed stand, and m is species proportion

(RP_{mix}; Table 4). In the same way, similar methods of weighting by species proportion can be calculated to compare other stand variables in mixed with monospecific stands (Forrester and Pretzsch 2015).

For such comparisons, the proportion of the species in the mixed stand (m_i) must be related to its available area, i.e. the species proportion by area. In this way, the productivity per hectare of a species in a mixed stand can be compared to the productivity per hectare of a reference monospecific stand. Using m_i without reference to the potential densities could lead to erroneous interpretations of the comparison between the productivities of species in monospecific and mixed stands (Dirnberger and Sterba 2014; Sterba et al. 2014).

Similarly, the ratio of productivity based on relative productivity (RPP) can be used to compare productivity in mixed versus monospecific stands (Harper 1977). This ratio gives the observed productivity (total yield or growth) in the mixed stand in relation to the productivity of the monospecific stands ($RPP = \sum P_{i,mix}/P_i$). The ratio $P_{i,mix}/P_i$ quantifies the required land area of pure stand to produce the same yield for the species i (as with the concept of A_i but in terms of productivity) and does not explicitly use species proportions. However, it may also be shown for varying species proportions. The RPP is equal to the relative yield total and land equivalent ratio which are common in herbaceous plant biology and agronomy (Vandermeer 1989, pp. 19–20).

Challenges and perspectives

Through this review of existing measures and indicators, we pave the way for a standardization process to characterize the structure, dynamic, and productivity in mixed forests at stand level. Standardization means common definitions and methods and thus facilitates comparable estimates, allowing an advance towards general theories,

but the process of standardization also involves certain difficulties (Köhl et al. 2000). It should be borne in mind that, as with monospecific stands, studies focusing on mixed stand structure, dynamics, and productivity at large spatial scales often use data from various research institutions or sources (e.g. Pretzsch et al. 2010, 2013, 2015b) and therefore the same standards must be applied from tree-level measurements to stand-level evaluation.

Strength of evidence when comparing mixed versus monospecific stands

If the methods for quantifying and evaluating stand structure, dynamics, and productivity in mixed forests are not standardized and tested in terms of their influence on mixing reactions, the strength of any evidence as regards mixing effects remains low. A unified characterization and evaluation of mixed stands should be described in such a way that monospecific stands can be interpreted as a special case, a boundary condition of the whole transect of species proportions. Besides certain methodological issues, there are a number of stand structure characteristics such as the horizontal and vertical distribution patterns of species that may have a strong influence on mixing reactions, which therefore should be considered (Forrester and Pretzsch 2015). Not including these characteristics in the analysis could lead to misinterpretations of the mixing effects (Leikola 1999; Schütz 1999). Therefore, many of the presented measures and methods need scrutiny of their effects on results at the stand level.

Most of the measures introduced in Tables 1, 2, 3, and 4 provide valuable information on both stand and species level. For example, when calculated for the stand level, measures of the size distribution (e.g. skewness, size differentiation index, Gini coefficient) indicate how mixed compared with pure stands as a whole come off regarding

spatial diversity, dimensions, and assortment yield of the stems, stand stability, and resistance. The same measures applied at the species level can reveal how the mixture modifies the role of the involved species when growing in mixed compared with pure stands. So, while the analyses at the stand level address the practical consequences of species mixing, analyses at the species level contribute to better understanding the effects found at the stand level.

Similarly, changes in net species interactions along abiotic gradients need further exploration considering the effect of using different methods to represent gradients. In mixed stands, species have different ecological traits and limitations, so the site conditions need to be specifically quantified in terms of the prevailing resources (light, water, mineral nutrients) and environmental factors (temperature, length of the growing season, etc.). The most limiting factors are generally better known in the case of pure stands, and therefore, these factors can be used to define the abiotic gradient for the analysis of mixed stands (Toïgo et al. 2015). However, this approach is complicated by the fact that it is not always easy to identify the environmental factors which have the greatest influence on complementarity (Forrester 2014). In a number of studies, site index has been used as a surrogate of abiotic gradients under the assumption that productivity is linked to abiotic gradients. In the absence of a specific site productivity index for mixed stands, the site index in pure stands was used (Pretzsch et al. 2010, 2013, 2015b). However, for certain species compositions, different patterns were found for the different species in the mixture, therefore making it difficult to interpret and generalize the results for the whole stand.

Methodological challenges

Tree-level measurements are often used to calculate stand-level variables. This requires the use of tree-level functions or form factors to estimate non-measured tree variables (e.g. tree volume, tree biomass), as well as functions for up-scaling from tree to stand level (e.g. height–diameter relationships). When applying these methods to mixed stands, the functions developed for pure stands are commonly used given the lack of functions adapted to mixed conditions. However, mixing can modify both tree allometry (Barbeito et al. 2014; Pretzsch 2014) and between-tree growth partitioning (Binkley et al. 2003; Pretzsch and Schütze 2014). Hence, it is necessary to either develop specific functions for mixed stands or improve the available tools for pure stands to extend their use to mixed stands (Forrester and Pretzsch 2015). However, due to the small number of long-term experiments in mixed stands, the information available is still scarce. Moreover, the high variability in stand structure in mixed stands could involve

different effects on tree allometry for a given composition, so further research is needed into the effect of species composition on tree allometry and resource partitioning.

Furthermore, a greater knowledge of the measures and indices of some of the stand characteristics is required as well as a clearer understanding of the implications of applying them. For example, different approaches can be used to estimate species proportions and the best approach to use may depend on the objective pursued. Thus, the proportion of the species by tree number may be important when analysing the survival and fitness of the species cohort; the species' share of the stand surface area may be best when the focus is resource acquisition and growth, while the number of functional groups may be of interest when evaluating resistance and resilience. Studies that compared different approaches to estimate species proportions using the same data (Pretzsch 2009, pp. 359–360; Huber et al. 2014; Dirnberger and Sterba 2014) clearly demonstrated that different approaches result in different proportions, which involve differences in the subsequent analysis. Differences in growth dynamics, not only between species but also within the same species for mixed and pure stands (Pretzsch 2005), lead to changes in species proportions over time, and hence, care must be taken when analysing long-term data (Puettmann et al. 1992).

As regards site productivity, finding a comprehensive indicator for mixed stands continues to be a challenge although three basic properties have been identified: (1) the indicator must be independent of age structure, (2) it should be a good descriptor of the site properties, and (3) it should be correlated with total biomass production and represent all the mixture effects along environmental gradients. The fact that for certain mixtures, over-/underyielding varies with productivity gradients, taking pure stand productivity as a reference (Forrester et al. 2013; Pretzsch et al. 2010, 2013; Toïgo et al. 2015), underlines the need for a specific productivity indicator for mixed forests.

Another challenging area concerns maximum stand density and self-/alien-thinning in mixed forests. Firstly, accurate estimations of MSDR in pure stands are required for each of the species in the mixed stand in order to calculate relative density indices and the area occupied by each species; secondly, the size–density trajectories and their dependence on species composition need to be understood for different mixtures; and finally, a stand density index based on the MSDR must be defined in such a way that it integrates the stand density in pure stands as specific cases of mixed stands.

The maximum stand density of a tree species on a given site is essential information for the assessment of site productivity, for modelling and prediction of stand dynamics, and for silvicultural regulation. Any deviation from the weighted mean line based on the pure stands

indicates that the mixed stands can carry more or less trees of a given size per unit area. And this is of course relevant for the assessment of the density and yield level, for development of silvicultural guidelines such as stand density diagrams (SDMD), and for forest modelling.

Improving the data base

Many of the abovementioned challenges require good quality data availability to explore and test the measures and methods presented. This implies long-term data for different stand structures (density, compositions, spatial patterns, etc.), site conditions, and development stages. However, certain kinds of species mingling (individual tree, group, cluster) are hardly ever included in mixed stand experiments and the same is true with regard to proportions of mixtures (10:90, 50:50, 90:10), thinning (degrees, types and sequences), or even combinations of these different experimental factors. Moreover, when experiments include mixed and pure stands, these should have similar characteristics, i.e. *ceteris paribus* conditions, as in studies based on triplets (Pretzsch et al. 2015b). This condition makes it hard to find appropriate sites for establishing this kind of experiment and adds further complications to the inherent problems associated with maintaining long-term experimental plots due to both natural and anthropogenic disturbances. When experiments with *ceteris paribus* conditions are not available for the different mixtures, a possible approach is to use inventory data and modelling techniques (del Río and Sterba 2009; Vallet and Perot 2011). However, certain aspects such as size–density trajectory or changes in mixing effects with stand development involve long-term monitoring, which is only possible with permanent plots.

From scientific analysis to practical application in silviculture

Although this paper reviews measures for describing mixed stands, analogous measures are required to quantify silvicultural prescriptions and guidelines. These are necessary in order to compare experimental trials as well as to achieve an optimal regulation of tree species density, the share of each species, and the form of intermingling depending on the goal defined by forest management practice (Assmann 1967).

For pure stands, numerous thinning experiments established in the past century exist which provide consolidated thinning theory as well as thinning guidelines for forest practice. This has led to the development of several indices to quantify and characterize thinning regimes, i.e. the degree, type, and sequence of thinning operations, as well as standards for evaluating thinning experiments. However,

some of those indices and methods may be not suitable to describe and evaluate thinning in mixed forests and therefore need to be modified or complemented for application in mixtures.

The dependency of the mixed stand characteristics (and therefore of the respective silvicultural guidelines) on site conditions must be given special consideration because, as in pure stands, the structure, dynamics, and productivity depend strongly on them. While neglecting the site effect may result in variations in growth in pure stands, it may cause complete loss of a species in mixed stands due to changes in interspecific competition. Therefore, for a given tree species composition, management guidelines adapted to the different site conditions should be developed.

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