

REVIEW

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# Toward managing mixed-species stands: from parametrization to prescription

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## Abstract

A better understanding and a more quantitative design of mixed-species stands will contribute to more integrative and goal-oriented research in mixed-species forests. Much recent work has indicated that the structure and growth of mixed species forests may fundamentally differ from monocultures. Here we suggest how to progress from the present accumulation of phenomenological findings to a design of mixed-species stands and advanced silvicultural prescriptions by means of modelling. First, the knowledge of mixing effects on the structure and growth at the stand, species, and individual tree level is reviewed, with a focus on those findings that are most essential for suitable modelling and silvicultural designs and the regulation of mixed stands as opposed to monocultures. Then, the key role of growth models, stand simulators, and scenario assessments for designing mixed species stands is discussed. The next section illustrates that existing forest stand growth models require some fundamental modifications to become suitable for both monocultures and mixed-species stands. We then explore how silvicultural prescriptions derived from scenario runs would need to be both quantified and simplified for transfer to forest management and demonstrated in training plots. Finally, we address the main remaining knowledge gaps that could be remedied through empirical research.

**Keywords:** Multiplicative mixing effects, Overyielding, Overdensity, Modelling mixing effects, Scenario analysis, Silvicultural prescriptions, Practical guidelines

## Background

For some time now, the forestry profession has been the subject of competing, and often conflicting, societal demands (Jensen and Everett 1994, Schmithüsen 2007). In addition, lower appropriations of resources in terms of personnel and budget allocated toward forest research and management activities have compounded increasing demands on managed forests to sustainably provide goods and services, including clean water, perpetually high levels of biodiversity, and resiliency and adaptability to the impending effects of climate change (Knoke et al. 2008, Kuuluvainen 2009). Recent research into stand dynamics following natural disturbances, combined with an increasing awareness of the ecological shortcomings and/or outright economic failures of many monocultures, has indicated that heterogeneous, structurally complex, mixed-species stands may surpass many

monocultures at meeting society's expectations for the sustainable provision of ecological, economic and socio-cultural forest goods and services (Bauhus et al., 2017a, b, Hector and Bagchi 2007). Although a few of these contemporary results of the benefits of heterogeneous mixed forests had already been anticipated by some silviculturists nearly a century and a half ago (Gayer 1886), for many decades the forestry profession in many parts of the world (Holvoet and Muys 2004), and particularly in Central Europe (Biber et al. 2015), strongly favored the establishment and management of mono-specific forests (Carnol et al. 2014, Hanewinkel 2001). Thus, societies with historically even-aged, mono-specific management approaches are increasingly challenged to restore and increase species heterogeneity and transform large forested areas back to mixed-species stands (Ammer et al. 2008), whereas the overarching concern in many natural (unmanaged) tropical, subtropical, and boreal forest ecosystems is the impending loss of high levels of species heterogeneity in response to exploitative forest management approaches (Liang et al. 2016). In both mono-species and poly-species

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forestry, suitable silvicultural prescriptions that ensure the long-term maintenance of mixture and structure are required; in mono-species forestry to re-establish stable and productive forest stands, and in poly-species forestry to avoid further losses of diversity and structure.

In many temperate forests, close-to-nature management approaches have gained widespread public support and have already led to considerable changes in silvicultural approaches. Although silviculturists have increasingly incorporated natural processes, biological legacies, and biological automation (Schütz 1997) into their management, quantitative silvicultural guidelines that facilitate efficient management are still largely limited to even-aged, homogeneous mono-specific stand types (Bauhus et al., 2017a, b). Silvicultural guidelines for mixed species stands are, if available at all, still predominantly vague and qualitative, and thus inadequately goal-oriented (Oliver and Larson 1996). Current guidelines for managing mixed-species stands are therefore excessively normative, focussing, for example, on selecting, tending, fostering and harvesting 100 crop trees per hectare (Schröpfer et al. 2009, Utschig et al. 2011).

A primary obstacle to the development of quantitative silvicultural guidelines for mixed-species management has been the fragmented nature of the currently available quantitative information about mixing effects and stand dynamics. Although the silvics of tree species are very well understood and stand dynamics have been retrospectively analyzed for many mixed-forest types (e.g., Oliver and Larson 1996), monocultures are typically the only forest types for which quantitative information on tree and stand growth dynamics is available. It may thus be tempting to broadly base management guidelines for mixed-species stands on extrapolations of models for monocultures (e.g., on yield tables or individual tree models). However, extrapolating results from these models relies on the assumptions that the individual species in mixed stands behave like they do in pure stands and that mixed stands behave like monocultures. While this would enable a simple projection of mensurational parameters (i.e., stand growth) and structure as a simple weighted mean of the parameters obtained in the respective pure stands, recent research has shown that stand dynamics and system responses in mixed stands seem to be far more complex and would be poorly captured with this approach (Pretzsch et al. 2017).

Researchers have thus begun to more systematically investigate the effects of tree species mixing on stand growth and productivity, stand structure, and stand dynamics (Zenner et al. 2012, Scherer-Lorenzen et al. 2005, Pretzsch et al. 2010, Pretzsch et al., 2017, Forrester 2014) as well as to re-evaluate risk distribution (Knocke 2017, Knocke et al. 2008), resource efficiency (Richards et al. 2010), and the functional significance of species diversity

(Scherer-Lorenzen et al. 2005). Research results support the general conclusion that stand and species productivity (Liang et al. 2016), size distribution and stand structure (Pretzsch and Schütze 2015), and tree allometry (Forrester et al. 2017) of mixed-species stands are quite different from the weighted mean of the respective pure stand constituents. While some evidence points to conditions under which mixed species stands are able to produce more volume (overyielding) than the monocultures of the respective constituent species, this is not necessarily the case for just any combination of tree species (Forrester 2014, Forrester and Pretzsch 2015). To overyield, species must exhibit complementary traits in terms of, for example, light requirements/shade tolerance or root depth. While these results are encouraging for the further expansion of mixed-species stands from the point of view of productivity or long-term carbon storage in timber, important silvicultural questions (e.g., natural regeneration [Zenner et al. 2005] or growth after release from competitors [Zenner and Puettmann 2008]) have yet to be more systematically explored in greater detail. Our knowledge of the dynamics and stand growth of most species combinations is far from complete and there are still no general guidelines for choosing species with appropriate complementarity or for designing temporal or spatial associations or separations of the associated species when establishing mixed species stands. Further, there are no quantitative guidelines for regulating mixing proportions, mixing patterns and vertical structures as well as prescriptions for regulating stand densities and scheduling (optimal timing) early and subsequent individual tree releases through thinnings.

To overcome the disjunction of quantitative knowledge about mixing effects, even for the most common tree species combinations, information needs to be integrated into a larger framework if it is to improve our understanding of mixed species stand dynamics and become more easily accessible for management. Thus far, the scope of most studies has been limited to investigating if any significant differences exist between the productivity of mixed stands and monocultures. The significant deviation of the growth and structure of mixed-species stands from the weighted mean of monocultures, however, underlines that the dynamics of mixed-species stands cannot be simply predicted by models developed for monocultures (Forrester and Tang 2016, Pretzsch et al., 2015a). To properly design the establishment and management of mixed-species stands, we thus need models that take into consideration already known relevant mixing effects. Such models will be essential tools for the development of silvicultural prescriptions by scenario analysis and for the quantitative formulation of guidelines.

One type of growth model that could be used to estimate multi-species, all-aged forest population structures is transition (rate) matrix models or simple matrix

models, which were first developed over 50 years ago by Lewis (1942) and Usher (1966). Introduced into forestry by Buongiorno and Michie (1980), this type of model has gained particular popularity for the management of uneven-aged and mixed-species stands. Computer simulation programs based on matrix models, which are neither individual-based nor process-based (Liang and Picard 2013), have been developed for various kinds of forests (e.g. Liang et al. 2006). Furthermore, Markov Decision Process models (MDP, e.g. Buongiorno 2001) have been developed to reduce the non-linearity and structural complexity of matrix models for broader-scale applications. However, because matrix models are based on the tree population structure rather than on individual tree competition, structure, and growth, they are not readily applicable for the integration of individual tree based silvicultural guidelines.

Alternatively, potentially relevant individual tree growth models for both mono- and mixed-species stands have become very common in recent decades (Burkhardt and Tomé 2012, Pretzsch et al. 2002). For monocultures, silvicultural guidelines for appropriate and goal-oriented stand establishment, tending, and thinning schedules are increasingly based on scenario analyses using well-supported individual tree growth models (Hasenauer et al. 2006, Hynynen et al. 2005, Nagel and Schmidt 2006, Pretzsch et al., 2015a) based on, and parameterized with, data from long-term experimental plots or inventory data. For mixed-species stands, however, equivalent models are available but hardly any quantitative silvicultural guidelines for the establishment and management of stands of different species mixtures have yet been developed (Bauhus et al., 2017b). We focus here on the individual tree growth models that are most suitable for the integration of individual tree related silvicultural guidelines (Burkhardt and Tomé 2012, Pretzsch et al. 2002).

To aid the integration of these various, fragmented mosaic pieces of knowledge into a targeted, goal-oriented pursuit to fill knowledge gaps for the quantitative design of mixed-species stands, this review (i) summarizes the main mixing effects found at the stand, species, and individual tree level, (ii) outlines the role of models for the design and development of quantitative silvicultural guidelines for mixed-species stands, (iii) addresses the main model components that need to be adapted to more realistically project mixed-species stands behaviour, (iv) introduces the main aspects and criteria for deriving quantitative silvicultural prescriptions and guidelines based on scenario analyses, and (v) elaborates the primary remaining knowledge gaps and how to remedy them with future empirical research. This review mainly addresses more or less even-aged mixed stands, because basic information about mixing

effects is currently only available for these stands and these are precisely the type of stands that are expanding in many countries that have turned away from monoculture forestry. In this review, we exclude mixing effects and mixing regulation in the very early stand development phase, including the browsing issue (Ammer 1996), as this has been reviewed elsewhere (Greene et al. 1999, Puettmann and Ammer 2007).

### **Review of the effects of species mixture on stand growth and structure**

A highly relevant finding for practitioners is that mixed stands can often produce more stem volume than the weighted mean of neighbouring monocultures (i.e., overyielding), or even more than is achieved by the most productive species of the respective assemblage when in monoculture (transgressive overyielding). Evaluations based on long-term experiments and inventory data have documented an average overyielding of 10–30% (Pretzsch and Forrester 2017). The main causes of mixing effects and overyielding are thought to be the complementary exploitation of crown and root space (Kelty 1992, Pretzsch 2014), the hydraulic lift and hydraulic redistribution (Prieto et al. 2012), the increased availability of mineral nutrient supply through deep rooting or atmospheric N<sub>2</sub> fixation (Bauhus and Messier 1999, Forrester et al. 2006, 2007, Gaiser 1952, Puhe 2003, Stone and Kalisz 1991), the temporal and spatial complementarity of niches (Forrester 2014), uptake and use efficiency of resources (Liang et al. 2015) and growth (Goisser et al. 2016), and the modification of growth partitioning and allometry of trees in inter-versus intraspecific neighbourhoods (Bayer et al. 2013, Thurm et al. 2017, Zeller et al. 2017).

As complementary resource use is the main cause of additional production, the most promising approach for enhancing volume (biomass) production is the mixing of light-demanding with shade-tolerant species, shallow-rooting with deep-rooting species, fast-growing with slow-grower or deciduous with evergreen species. The benefit of mixing may change with site conditions, however, as it likely depends on the potential of the species assemblage to compensate for the respective growth limiting factor of a given site. Thus, on moist and fertile sites, where light is the limiting factor, combinations of light-demanding and shade-tolerant species may be most beneficial. On dry and nutrient poor sites, in contrast, combinations of deep- and shallow-rooting species may remedy the soil-based resource limitations. Although reported overyielding in volume growth of about 10–30% for commercial tree species in temperate and boreal zones appear moderate in comparison to overyielding of up to 50% found in the subtropics and tropics and for atmospheric nitrogen fixing tree species (Forrester et al. 2006, 2007, Kelty 1992), they are nevertheless highly relevant because they can be obtained

simply by a smart mixing design. In contrast, the benefits derived from thinning are often lower and require repeated silvicultural entries (Assmann 1970). Overyielding represents a higher efficiency of space use in that a given area of mixed stands yields more stem wood volume and fixes and stores more carbon than equivalent areas of monospecific stands. Of special interest for forest practitioners are mixed-species stands achieving transgressive overyielding, which could result in gains of up to 30% if the tree species mixture is complementary (Pretzsch and Forrester 2017). As a consequence, annual allowable cuts, and the volumes removed and remaining standing, may change compared with monocultures.

Table 1 summarises the overyielding of common two-species assemblages in Central Europe and underlines the fact that the mixing effects are not only scientifically evident but also practically relevant. Long-term experiments show that in relation to the weighted mean of the monospecific stands, mixed-species stands produce 11–30% more stem volume (Pretzsch 2016). Combinations of more similar species (e.g., Norway spruce and European beech, Norway spruce and silver fir) result in lower overyielding than complementary species combinations (e.g., Scots pine and European beech, European larch and European beech). In addition to the means and standard errors of overyielding, Table 1 presents conservative correction factors that may be used to estimate mixed stand productivity based on the productivity of neighbouring monocultures of the constituent species. The correction factors that apply for fully stocked mixed-species stands of individual to groupwise mixing patterns at mixing proportions of about 50:50 indicate that the productivity of monocultures should be multiplied by 1.10–1.20 to obtain an estimate of the productivity of the respective mixed-species stands.

Mixing tree species can also significantly increase the maximum stand density compared with monospecific stands (Fig. 1), resulting in overdensity in terms of tree numbers per hectare (Amorosos and Turnblom 2006), stand basal area (Wellhausen et al. 2017), stand density index (Pretzsch and Biber 2016), or standing volume (Bielak et al. 2014). An interesting finding is that while mixing has a strong effect on the horizontal yield component such as stand density, it has often no significant

effect on the vertical yield component in terms of stand height growth (Vallet and Perot, 2016). The increase in density rather than height means that mixing can raise stands to higher levels of the standing volume-stand height relationship (rule according to Eichhorn 1902) and the total volume yield-stand height relationship (yield level according to Assmann 1970). However, Pretzsch and Forrester (2017) showed that the overyielding of mixed versus mono-specific stands is mostly based on both an increased stand density and an accelerated volume growth rate of the trees.

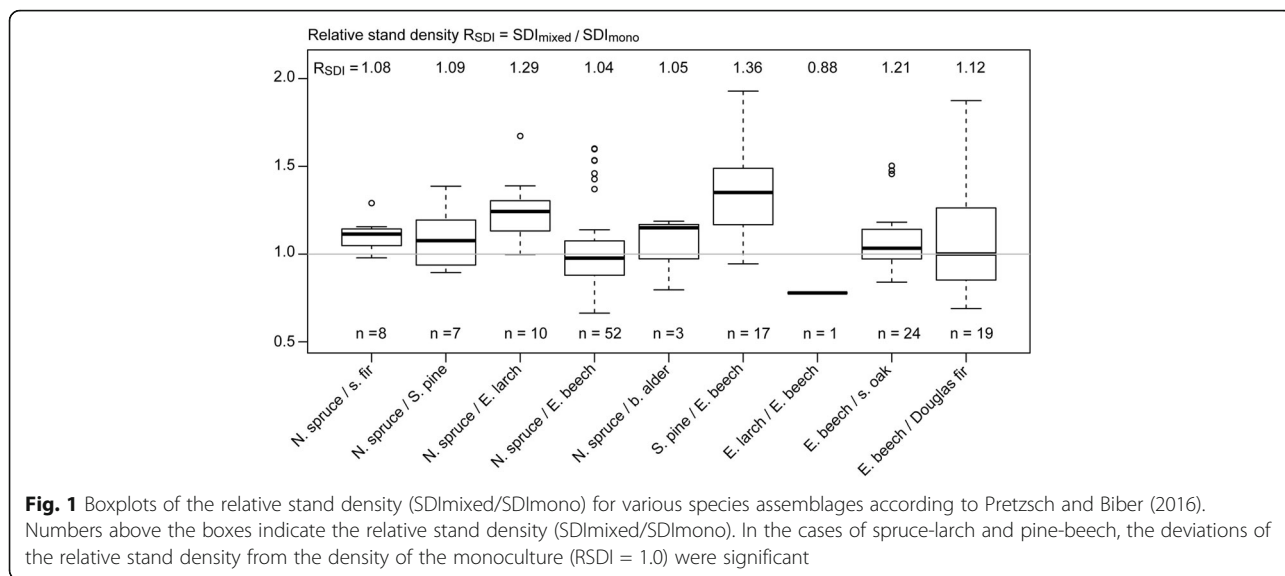
The increase in maximum density is reflected by an increased level of the self-thinning line and a reduction of tree mortality in mixed stands (Pretzsch and Biber 2016). However, beyond the level of the self-thinning line, mixing can also modify a stand’s self-thinning slope. Especially tree species with a low self-tolerance according to Zeide (1985), such as European beech, may benefit from mixture by the reduction of intra-specific competition and a flattening of the self-thinning line. This occurs at the expense of the admixed species whose self-thinning line becomes correspondingly steeper. So, the self-thinning of one species may be reduced as its competitive effects turn into alien-thinning, i.e., inter-specific competition.

Given complementarity of morphological and physiological traits, the canopy space of mixed species stands can be much more densely packed than in monocultures (Jucker et al. 2015, Pretzsch 2014). The tree size distribution can be wider (Fig. 2), the vertical layering more heterogeneous (Dănescu et al. 2016, Peck et al. 2014), and the asymmetry of competition higher (Pretzsch et al., 2016a, b), even though growth dominance is similar to monocultures (Pretzsch et al. 2017, Binkley et al. 2006). Especially in mixtures in which one species takes the lead in size growth and suppresses that of the other, the height growth curves may differ from those in pure stands (Wellhausen et al. 2017). Often, one species can significantly accelerate while the other significantly slows down in height growth, so that the weighted mean height of the species assemblage remains similar to monocultures (Vallet and Perot, 2016, Pretzsch et al., 2016a). A mechanistic explanation of this effect of inter-specific competition is still missing. However, this kind of height growth

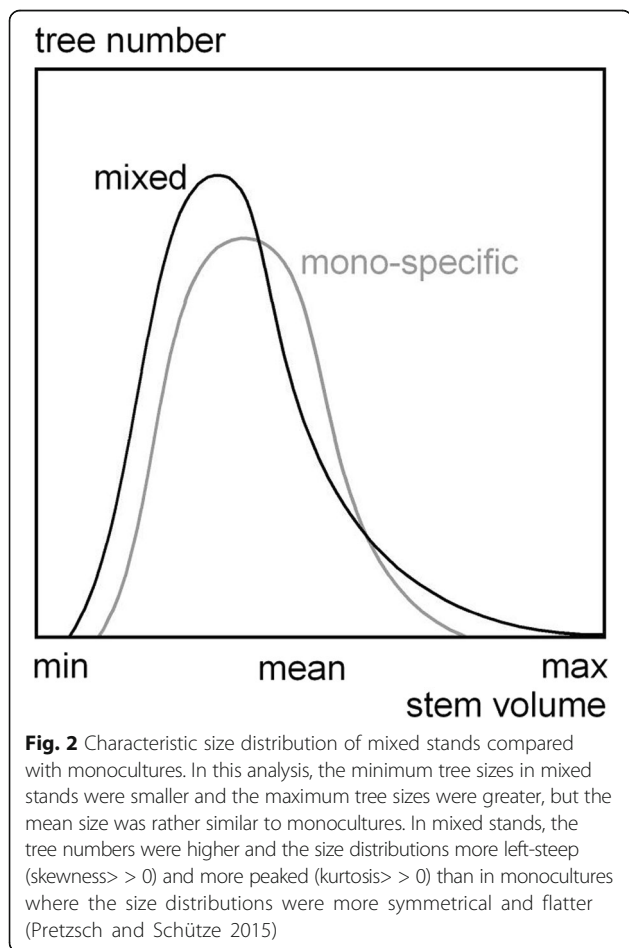
**Table 1** Mixing effects on stand productivity of various tree species mixtures in Central European forests derived from long-term experiments (Pretzsch and Forrester 2017). The relative overyielding (%) refers to the productivity of the mixed species stands in relation to the weighted mean of the neighbouring monospecific stands. The correction factors may be used to conservatively adjust the stand productivity of monospecific stands to the expected stand productivity of the respective species assemblages (Pretzsch 2016)

Species combination	N. sp./E. be	S. pi/E. be	s. oak/E. be	E. be/D-fir	S. pi/N. sp	E. la/N. sp	N. sp/s. fir	Mean
Overyielding (± SE) in	21 (±3)	30 (±9)	20 (±3)	11 (±8)	21 (±11)	25 (±6)	13 (±6)	
Corr. factor	1.10	1.20	1.10	1.10	1.20	1.20	1.10	1.10

N. sp. Norway spruce (*Picea abies* (L.) KARST.), E. be. European beech (*Fagus sylvatica* L.), S. pi. Scots pine (*Pinus sylvestris* L.), s. oak sessile oak (*Quercus petraea* (MATT.) LIEBL.), D-fir Douglas-fir (*Pseudotsuga menziesii* MIRB.), E. la. European larch (*Larix decidua* MILL.), s. fir silver fir (*Abies alba* MILL.)



**Fig. 1** Boxplots of the relative stand density ( $SDI_{mixed}/SDI_{mono}$ ) for various species assemblages according to Pretzsch and Biber (2016). Numbers above the boxes indicate the relative stand density ( $SDI_{mixed}/SDI_{mono}$ ). In the cases of spruce-larch and pine-beech, the deviations of the relative stand density from the density of the monoculture ( $RSDI = 1.0$ ) were significant



**Fig. 2** Characteristic size distribution of mixed stands compared with monocultures. In this analysis, the minimum tree sizes in mixed stands were smaller and the maximum tree sizes were greater, but the mean size was rather similar to monocultures. In mixed stands, the tree numbers were higher and the size distributions more left-steep ( $skewness > 0$ ) and more peaked ( $kurtosis > 0$ ) than in monocultures where the size distributions were more symmetrical and flatter (Pretzsch and Schütze 2015)

response means that in mixed-stands, species-specific height curves reflect competitive conditions rather than site conditions. In uneven-aged stands, some trees are able to endure for decades with little height growth, reaching just 10 m at age 100. Consequently, height loses its indication of site quality and the typical site indexing by height-age relationships becomes questionable (Wiedemann 1951, pp. 131–133).

Whether a given mixture can exploit the potential for complementary and overyielding on a specific site also depends on the stand structure (Dănescu et al. 2016, Zhang and Chen 2015). Obviously, combinations of shade-tolerant and light-demanding species can only exploit the complementarity when the light-demanding species is taller than the shade-tolerant species, and when this pattern is maintained as stand development progresses (Zenner et al. 2012). The relative height of a species in a mixed stand may be even more relevant for its growth and overyielding potential than the given site conditions (Pretzsch et al., 2013, Pretzsch et al., 2015b). The presence of species in different canopy layers and their mixing proportions depends very much on their respective competitive strengths and how this relationship changes with the site conditions. While site conditions certainly determine the productivity and structure (but not the survival or existence of the species) in monocultures, they are also highly relevant for the abundance, survival, and wood quality of the species in mixed stands. In monocultures, any precarious interspecific competition is simply eliminated, so models do not have to account for the effect of specific species combinations on productivity. However, in mixed stands it becomes relevant that a species' productivity may be determined much more by the competition of its neighbours (conspecifics and other species) than by the site conditions directly.

Tree species mixing and structural heterogeneity may modify tree morphology (Fig. 3) and thereby wood quality (Metz et al. 2013, Zeller et al. 2017). Biomass and leaf area allometry of trees are strongly affected by the spatial tree distribution within a stand (Forrester et al. 2017) and it is rather the stand structure than the species identity that is responsible for the difference in allometry of trees between mixed and monospecific stands (Pretzsch and Rais 2016). Mixing often increases crown width (Bayer et al. 2013, Juchheim et al. 2017), crown length (Pretzsch 2014) and the leaf mass (Forrester et al. 2017) of crowns compared with monocultures, but can decrease the root-shoot allometry (Thurm et al. 2017), wood density (Zeller et al. 2017), and stem slenderness (Wellhausen et al. 2017).

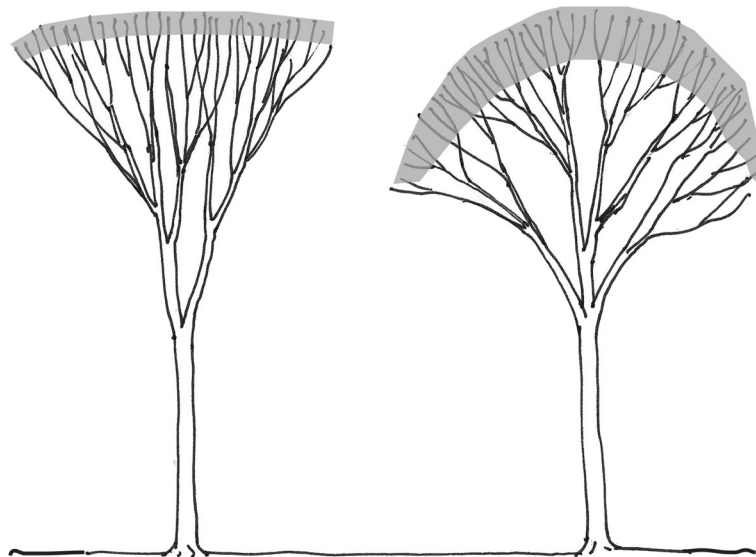
Bauhus et al. (2017a) reviewed the effects of tree diversity on the resistance and resilience of forests in relation to a number of abiotic (drought, wind, fire) and biotic (insect herbivores, pathogens) stress and disturbance factors. Compared with monocultures of susceptible or less resilient species, mixing more resistant or resilient species with less susceptible and less resilient species can reduce damage or lessen the reduction in ecosystem function following some biotic disturbances. However, storm, fire, or drought damage to individual species may not be reduced in mixtures when compared to monocultures (Knoke 2017, Metz et al. 2016, Grossiord et al. 2014a, b). There is more evidence for beneficial diversity effects in relation to biotic disturbance agents (Bauhus et al., 2017a, b). Managers should be aware that mixtures do not provide universally higher resistance or resilience to disturbances than monocultures. In most cases, it depends to a large

extent on the attributes of the species in mixture in relation to the specific disturbances.

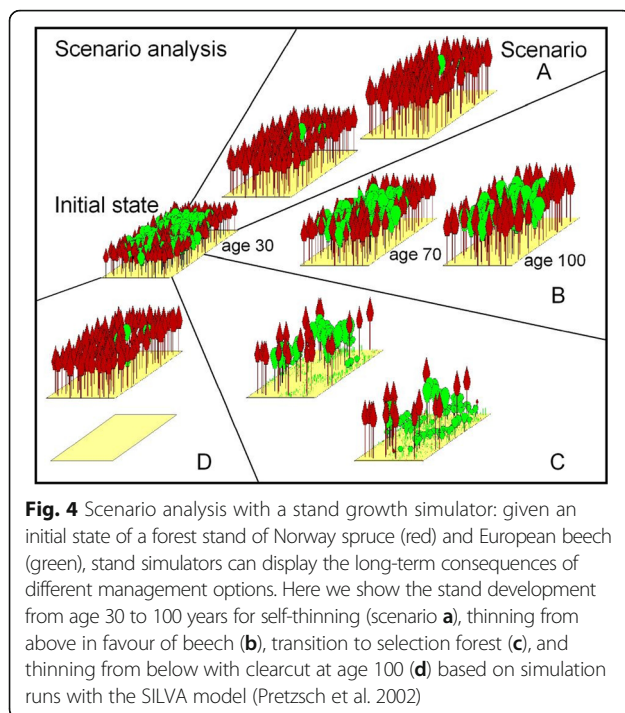
### The use of stand simulators for developing silvicultural prescriptions

As this section deals with the key role of stand growth models, stand growth simulators, and scenario calculations for designing mixed species stands, we first define the respective terms. A stand growth model is the result of abstracting and biometrically reproducing a real forest stand. When the biometrically formulated algorithms are converted into a useful computer program, a stand growth simulator is created that, with the help of the computer, can reproduce the behaviour of the forest stand and be used to perform scenario runs for various initial conditions and silvicultural treatments (Burkhardt and Tomé 2012, Gadov and Hui 2001, Weiskittel et al. 2011).

Through the organisation, synthesis and utilisation of knowledge about forest growth, growth simulators can expand both the basic and applied knowledge required in forest management and forest science equally. Both growth models and simulators are based on, and parameterized with, data from long-term experimental plots or inventory data. Due to the longevity and complexity of forests, stand growth simulators have become essential for, among other things, prognoses of wood volume revenues, prediction of sustainable annual cuts, and for the development of silvicultural prescriptions to elucidate silvicultural pathways (Oliver and O'Hara 2004) (Fig. 4). Because it would simply take too long to realize and empirically compare several treatment options by first establishing long-term experiments and then selecting



**Fig. 3** Whereas European beeches in monocultures (left) develop steeper branches, those growing in mixture (right) with Norway spruce have more branches, less steep branches, and nearly twice the number of second and third order branches (Bayer et al. 2013)



those with the most convincing results, we focus our attention in this section on the latter use of simulators. While experiments may require decades until the desired information is available (Zenner et al. 2011) stand growth simulators can do this much faster, albeit perhaps with less certainty (von Gadow 1996).

For monocultures, the silvicultural guidelines for appropriate and goal-oriented stand establishment, tending and thinning are routinely based on scenario analysis with growth models (Pretzsch et al. 2008). Scenario runs have been successfully employed to develop silvicultural prescriptions for Norway spruce (Courbaud et al. 2001), Scots pine (Rojo et al. 2005), and for mixed conifer and broadleaved stands (Thurnher et al. 2011). Such scenario analyses typically start with a broad set of initial stand conditions (e.g., initial density and spacing, site conditions) and silvicultural options (e.g., starting values, stand density level, number of future crop trees, mixing proportion), are intended to reveal long term consequences of treatments on various forest functions and services (Biber et al. 2015), permit the selection of options of interest (Puettmann et al. 2015) and the sensitivity to silvicultural interferences (Gadow et al. 2009), and finally enable a down-select to a restricted number of the most suitable prescriptions for a spectrum of site conditions (e.g., best, medium and poorest sites) and objectives.

Owing to the lack of knowledge and integration of historically fragmented research efforts, equivalent individual tree growth models for mixed-species stands are

either entirely missing or are currently only in the development stage. As a consequence, guidelines for the design and management of mixed-species stands are often based on models for monocultures of the constituent species, e.g., on yield tables, assuming that (1) mixed stands behave like monocultures and (2) their growth and structure equals the weighted mean of neighbouring monocultures. Alternatively, the guidelines may be simply normative and focus on the tending, fostering and harvesting of 100 crop trees per hectare, without taken into consideration whether those 100 trees over- or underexploit the site-specific capacity (Schröpfer et al. 2009, Utschig et al. 2011). In this regard, most thinning prescriptions for mixed-species stands are still qualitatively vague, trial and error-like, and fail to exploit available knowledge about mixed-stand dynamics.

Due to the complexity of the task and the variety of options available, the design of mixed-species forest stands and the development of goal-oriented quantitative silvicultural prescriptions depend on appropriate models, simulators, and algorithms for silvicultural regulations. Scenario analyses and the resulting guidelines for the design of mixed-species stands should ideally consider the entire life cycle of the stand, including how to initially establish, tend, thin, and again regenerate a mixed-species stand after the final harvest. The establishment and management after clearcutting of mixed stands of Norway spruce and common alder or sessile oak and Scots pine are prime examples for starting in mixture right from the beginning of the rotation. Scenario analyses should also consider how to transform (or transition) existing monocultures into mixed-species stands. For this, the transition of existing Norway spruce monocultures into mixed stands of two species (following canopy openings in the mature stand phase to naturally regenerate spruce, coupled with underplanting of beech) is an important contemporary example.

Scenario analyses also facilitate the exploration of very crucial questions and challenges that arise when tree species are mixed. Frequent questions that arise in the context of mixed-species management are: How can species be kept in play by various temporal or spatial arrangements of the constituent species, while also ensuring the continued existence of a beneficial and complementary structure? How can desired mixing proportions be realized, regulated, and maintained over time? How are individual tree size growth and stand growth modified by stand density? Which trade-offs can be expected between the various forest functions and services, e.g., between species diversity and productivity, productivity and stability, or risk and productivity? How are quality and quantity of the produced wood linked with each other? How do various amounts of standing volume in the overstorey affect both the species

composition and the growth of the regeneration? These and other frequent questions from practitioners are much more difficult to predict in mixed stands than in monocultures and answers to these questions are often speculative at this point.

Algorithms for the regulation of mixed stands that are implemented in models are quite complex and would need to be simplified to be of use to forest managers. The prescriptions that are ultimately selected from multiple scenario runs would need to be translated into straightforward guidelines that capture the salient principles of the dynamics of the mixed species involved. Further, prescriptions should not be so complex as to result in paralysis or in unrealistic (i.e., too costly) management requirements. In addition, they should be complemented by training plots in the field in order to reveal and demonstrate the underlying treatment principles and regime.

#### **Further development of growth models for the design of mixed-species stands**

Growth models and simulators that integrate mixing effects and mechanisms are essential for designing future mixed-species stands. Although four modelling approaches have been identified that are suitable for deriving and predicting mixed-species forest growth dynamics (Pretzsch et al. 2015) and the general concepts for such models are under development (Forrester 2017), all four approaches are still plagued by critical knowledge gaps that need to be remedied by further research before realistic scenarios can be portrayed. A first approach, which derives the growth of mixed-species stands as a weighted mean of the monocultures based on models of the respective species, neglects any multiplicative mixing effects and interactions. A second approach, which indirectly incorporates mixing effects into individual-tree growth models by integrating species-specific competition indices, neglects that the tree allometry, maximum density and mortality can change as well. A third method, which directly incorporates mixing effects using multipliers that modify growth rates and stand density, requires data that are as yet available for only a very few species combinations. The fourth approach, which uses process-based models that represent mixing effects by incorporating within-stand environmental conditions, species-specific structures, and resource uptake and availability, is the most promising but still in the very early development phase (Forrester and Tang 2016, Rötzer et al. 2009).

As spatially explicit growth models and simulators have the potential to simulate the effect of the natural or man-made spatial and temporal arrangement of different tree species in a stand, these models are of special interest for the simulation of heterogeneous mixed forest stands. Although we specifically refer to such models in

this section, most of these considerations can be applied to models and simulators in general.

#### **Growth**

Due to positive inter-specific interactions, the potential size growth of trees can be higher in mixed- compared with mono-specific stands. Thus the curve systems for potential growth of tree height, diameter, and tree volume would need to be updated with data from long-term plots or inventory data that specifically include mixed-species stands. Further, competition indices, used to adjust potential to actual growth, need to consider the species identity of the neighbours present in the stand. Competition indices might need to be split into intra- and interspecific components such that, depending on the species identities of the neighbours in a stand, indices might express adverse competitive effects, neutral, or even reduced competitive effects (i.e., facilitation) by the different species. Although individual tree models can now rapidly simulate 3D structure, they currently do not consider that the tree allometry may differ between mixed and monospecific stands. Differing tree morphology, however, is relevant for the appropriate prediction of crown competition between the trees, stem volume, biomass production, and wood quality.

#### **Mortality and risk**

Mortality models are usually based on the self-thinning line as the upper threshold (stand level) or on minimum (threshold) growth rates needed for individual tree survival (individual tree level). Both the level (intercept) and the slope of the self-thinning line depend on site conditions and the associated species. As the stand density of mixed stands can significantly exceed monospecific conditions, species-specific self-thinning lines in mixed species conditions need to be updated and adapted to different combinations of species mixtures and site qualities. For the same species, minimum growth rates of individual trees required for survival (but perhaps not growth) may be lower in mixed stands due to reduced competition, necessitating adjustment and the reduction of thresholds for growth rates before the mortality function of the models predicts that a tree dies and drops out. In addition, the findings of effects of tree species mixing on the resistance and resilience of forests in relation to a number of abiotic (drought, wind, fire) and biotic (insect herbivores, pathogens) stress and disturbance factors need to be parametrized and integrated in models for mixed-species stands.

#### **Regeneration**

The interaction among trees in the regeneration layer, whether artificially or naturally regenerated, as well the interaction between understory and overstory trees need



to be integrated into growth models. Whereas models typically account for overstory effects that reduce levels of available light in the regeneration layer (Pretzsch et al. 2015b), the regeneration layer and the understory may in turn affect the overstory by taking up water and mineral nutrients (Knapp 1991).

Finally, future models should encompass a broader set of output variables that are associated with forest resources, trees/stand vitality and stability, production and regeneration, biological diversity and the fulfilment of additional functions such as protection and socio-economic uses. This would permit the effects of different silvicultural options on ecological, economic, and social functions of forests to be considered simultaneously, such that trade-offs can be analysed and decisions can be made more transparently to achieve multipurpose objectives tailored to the landowners' objectives.

### **Aspects and criteria for design and the silvicultural guidelines of mixed species management**

Apart from some rather normative crop tree concepts, quantitative guidelines for the establishment, thinning, and regeneration of mixed-species stands are generally lacking. By quantitative guidelines we mean instruction for initial density, spacing, mixing proportions, thinning or regeneration cuts for mixed-species stands based on dendrometric characteristics (e.g. species-specific tree numbers, stand areas, SDI, basal area, or volume per unit area for the development of the remaining and removal stand). Nonetheless, the findings described in the previous sections that touch upon, for example, niche complementarity, allometry, size and growth partitioning, mortality, overyielding, and overpacking are key components of future quantitative guidelines for mixed-species management via model application and scenario calculations. Silvicultural prescriptions derived by simulation and scenario analyses will need to be translated into straightforward guidelines that are sufficiently detailed yet not too complex for application. Here we see a particular need for further research. Algorithms underlying the implementation of the models that regulate mixed stands are very complex. Complex detailed models in themselves are not of great utility to forest managers, however. Rather, the output of complex models must be translated into meaningful parameters and simple instructions that are useful to forest managers. In the remainder of this section, we review silvicultural measures that are specific and essential for mixed-species stands, i.e., the different kinds and intensities of thinning and the selection and thinning of crop trees will not be included because this has been sufficiently described elsewhere (Assmann 1970, Burschel and Huss 1987, Oliver and Larson 1996).

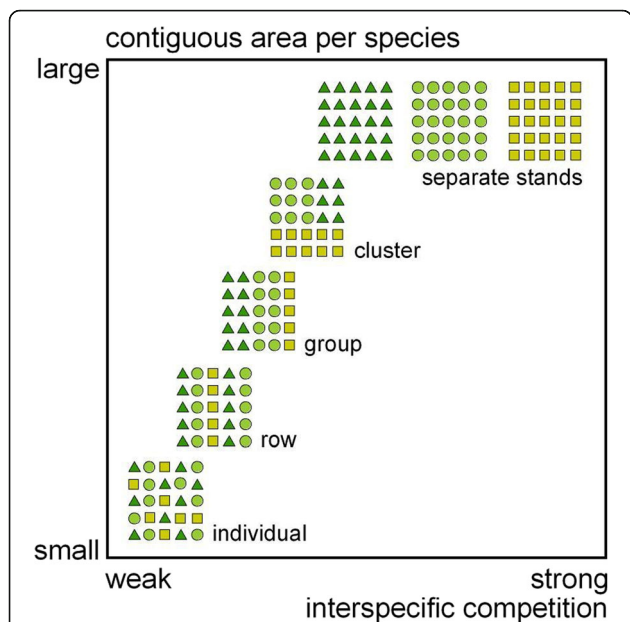
We think the simplified prescriptions for mixed-species stand management should contain guidelines for (i) choosing species with appropriate complementarity, (ii) designing the temporal or spatial association/separation of the associated species when establishing mixed species stands, (iii) regulating mixing proportions, mixing patterns and vertical structures, (iv) regulating stand densities, and (v) initiating regeneration by volume reduction in the overstory. The resulting guidelines for practitioners should be relevant, straightforward, and not overly complex, yet capture and portray the applied equivalent of the simulation model algorithms.

#### (i) choice of species combination

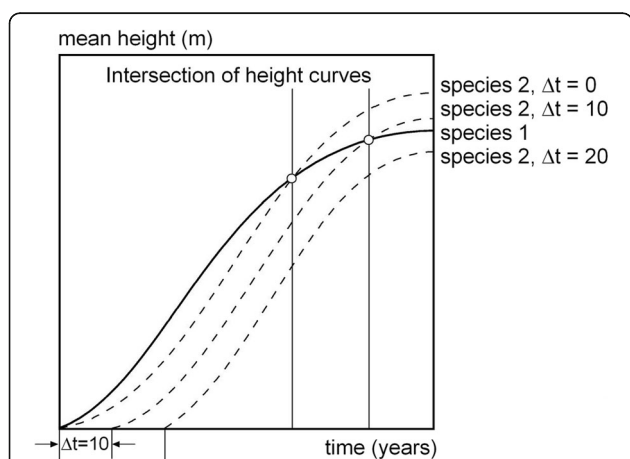
Combinations of species with complementary ecological traits have the potential for higher resource supply to trees and resulting yields compared with monocultures. Combinations of light-demanding and shade-tolerant species, shallow- and deep-rooting species, early and late successional species, and mixtures with N<sub>2</sub>-fixing tree species are likely to successfully improve yields. Increased yields may result from strong niche complementarity (e.g., by combining light-demanding species in the upper storey with shade-tolerant species in the understorey), supporting more trees per hectare (i.e., an increased maximum stand density) to forage. Such species combinations may result in further complementarity effects, if the species mixture also results in improved water supply due to the enhancement of the water holding capacity of the humus layer.

#### (ii) design of the temporal or spatial mixing pattern

Mixtures in which one species gets ahead in height growth and imparts a strong shading effect on the admixed species may cause strong alien-thinning, segregation/demixing or even the complete loss of one species. Inter-specific competition may be reduced and the mixture may be stabilized over time by spatially or temporally separating the constituent species (Figs. 5 and 6), i.e., by establishing each species in groups or clusters instead of intermixing the different species at the individual tree level, or by establishing the different species in different layers that have different ages instead of establishing a mono-layered mixture. Recognizing that stem and wood quality are not primarily determined by the mixture, but by the species-specific morphological plasticity and the structural heterogeneity of the stand, high wood quality in mixed stands may be achieved by increasing intra-specific competitive pressure on more plastic tree species or by spatially clustering species with similar traits and/or sizes in groups; less plastic species may achieve a reasonable wood quality even in heterogeneously structured, small scale individual tree-to-tree species mixtures.



**Fig. 5** Regulation of inter-specific competition by spatial separation of tree species. The stronger the inter-specific competition between the species, the more contiguous a growing space is required for the establishment and development of a species in a mixed stand. Inter-specific competition can be reduced by mixing of three species (represented by  $\Delta$ ,  $\square$ ,  $\circ$ ) in (from left to right) individual tree mixture, rows, groups, clusters, or separate stands (modified after Bauhus et al. (2017a, b))

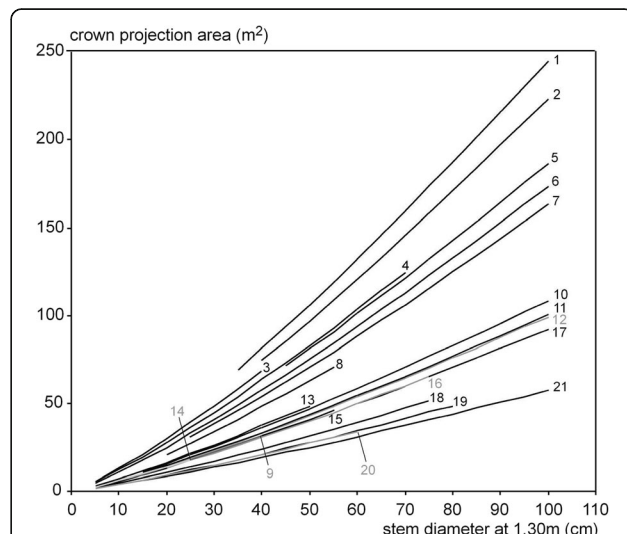


**Fig. 6** Regulating the structural setup and inter-specific competition by temporal separation. If tree species 2 is admitted to species 1 with a delay of  $\Delta t = 10$  or 20 years, the competitive pressure on species 1 can be reduced. The trajectory and the intersection of the species-specific height curves provide useful information for mixing design and regulation

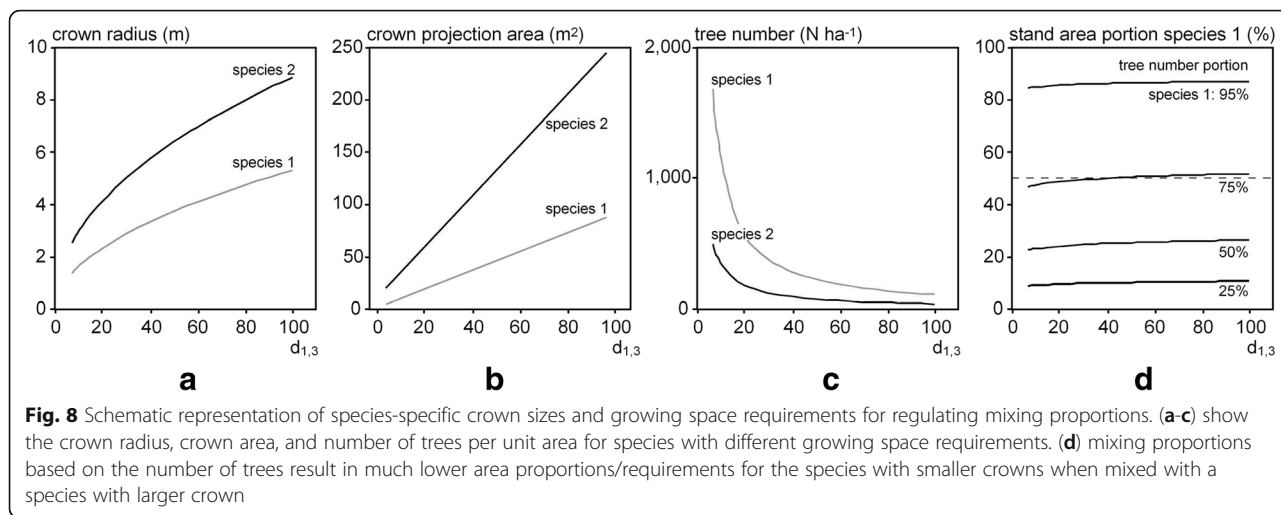
(iii) regulating mixing proportion

The quantitative regulation of mixing proportions requires information about the species-specific growing space requirements. Tree species with the same tree diameter can differ considerably in crown size and required growing space. Figure 7 shows this for selected tree species (1–21). Similarly, to achieve a desired tree number or standing volume per hectare, different species-specific growing space proportions may be required. Figure 6 shows that for a given tree diameter of 30 cm, the crown area and growing space requirements can vary between 10 and nearly 50 m<sup>2</sup> and, for a tree diameter of 100 cm, the range is between 50 and 250 m<sup>2</sup>. The relationship between the crown size and growing space requirements of different species can be quantified by equivalence coefficients that indicate, for example, how much growing space a beech may need on average in relation to a spruce of approximately the same tree diameter and stem volume.

The relevance of species-specific crown sizes and growing space requirements for the regulation of mixing proportions is illustrated in Fig. 8. When equal in tree diameter, species 2 (e.g., European beech) has a much larger crown radius and crown area (Fig. 8a and b, respectively) compared with species 1 (e.g., Norway



**Fig. 7** Tree species of the same tree diameter can differ considerably in crown size and required growing space. This is demonstrated for 1) *Quercus nigra* L., 2) *Platanus x hispanica* MÜNCHH., 3) *Carpinus betulus* L., 4) *Tilia cordata* MILL., 5) *Khaya senegalensis* (DESR.) AJUSS., 6) *Fagus sylvatica* L., 7) *Aesculus hippocastanum*, 8) *Robinia pseudoacacia* L., 9) *Alnus glutinosa* [L.] GAERTN., 10) *Araucaria cunninghamii* AITON ex. D.DON, 11) *Pseudotsuga menziesii* [MIRB.], 12) *Abies alba* MILL., 13) *Sorbus aucuparia* L., 14) *Betula pendula* ROTH, 15) *Acer pseudo-platanus* L., 16) *Abies sachalinensis* MAST., 17) *Quercus petraea* [MATT.] LIEBL., 18) *Pinus sylvestris* L., 19) *Larix decidua* MILL., 20) *Fraxinus excelsior* L., 21) and *Picea abies* [L.] KARST



spruce). Therefore, the potential number of trees per hectare is much lower for species 2 than for species 1 (Fig. 8c). In the mixed stand, proportions (by tree density) of species 1 of 25, 50, 75 or 95% need much lower area proportions (about 10, 25, 50, 85%, respectively) than species 1, indicating a lower growing space requirement compared with species 2. Thus mixing proportions based on the number of trees result in much lower area proportions for a species with smaller crowns when mixed with a species characterized by larger crowns.

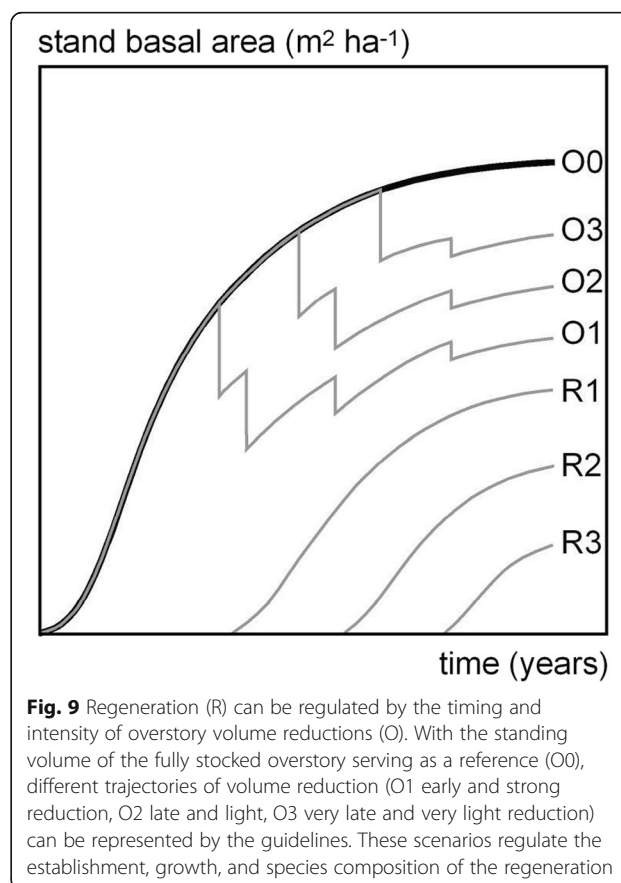
(iv) regulating stand density

Similar to monocultures, stand density in mixed stands may be regulated quantitatively using stand basal area, stand density or number of trees per hectare. Trajectories of the number of trees against mean tree diameter, number of trees against mean tree height, or stand basal area against stand age may serve as useful representations for guidelines. Analogous to monocultures, guidelines for mixed stands should detail species-specific density levels and additionally consider species-specific growing space requirements.

(v) standing volume reduction for initiation of regeneration

The initiation, development, and species composition of the regeneration can be regulated by the standing volume of the overstory. Figure 9 schematically represents various prescriptions that illustrate how regeneration (R) can be regulated using the timing and intensity of volume reductions in the overstory. The standing volume of the fully stocked overstory is used as a reference (O0). In this way, different trajectories of volume reduction

(O1 early and strong reduction, O2 late and light, O3 very late and very light reduction) can be represented in the guidelines. The options O1 and R1 represent an early start and strong acceleration of the regeneration. The later the overstory is opened and volume is reduced (O2 and R2, or O3 and R3) the less stable the remaining old stand becomes and the later the regeneration becomes established.



The above examples have detailed some of the most important components of a framework illustrating how mixed stand dynamics may be quantitatively regulated and incorporated into silvicultural guidelines. In this manner, scenario runs using computer models may yield successful treatment options that can later be transformed into simple guidelines that quantitatively address the most important aspects of mixed species management. Figure 10 exemplarily depicts stand management diagrams (see Newton 1997) for mixed-species stands that might result from scenario calculations and could serve as a core element of silvicultural guidelines for two-species mixed stands. To ensure that the species mixture is maintained over time, the trajectories of the two species should be kept in the white corridor. Entry into the grey hatched corridor should be avoided as it would mean the eventual loss of mixture and structural heterogeneity.

**Conclusions**

**Future research directions to improve understanding, prediction, and scenario calculations**

The near exclusive focus of quantitative silvicultural research on monocultures in the past has left scientists and practitioners with many unanswered questions that could be successfully addressed with mixed stand experiments that provide opportunities for linking quantitative analyses of stand dynamics with training Bauhus et al. (2017a, b). We see several research priorities that can serve to close knowledge gaps, improve simulation models, and pave the way for taking results from computer analysis to the design of mixed-species forests and application in the field. The following listing outlines our view of the most important knowledge gaps for modelling and regulating mixed species stands.

- Direct effects of mixing.

Because mixing effects can change with different proportions of the constituent species (20:80, 50:50, etc.), mixing patterns (individual tree mixture, group mixture etc.), and age structures (even-aged, tow-cohort type etc.), these factors need to be systematically incorporated into future experimental plots.

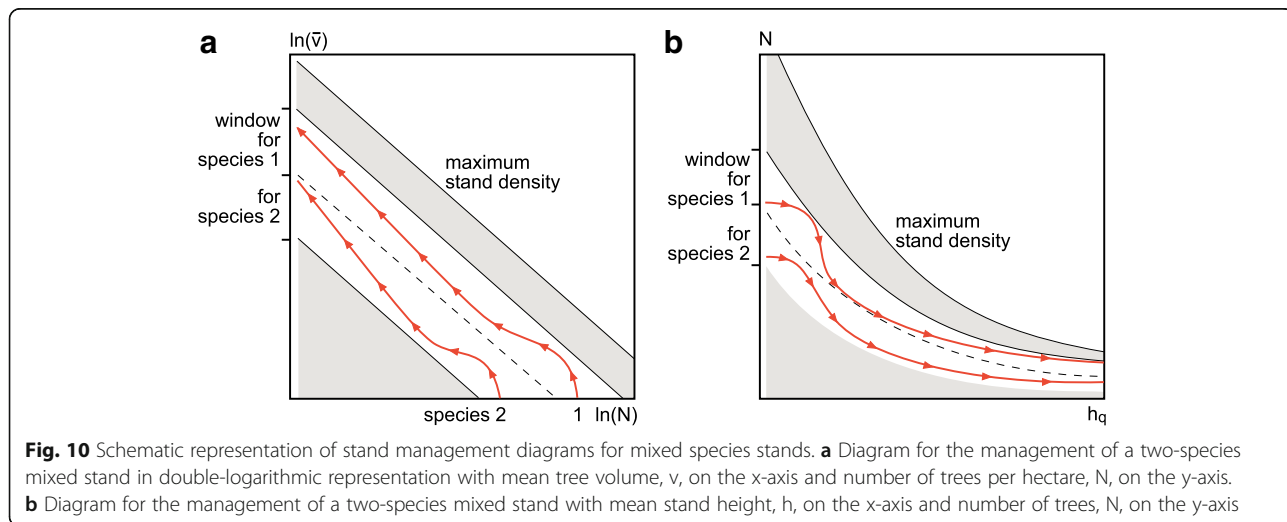
- Morphological changes of trees.

Although mixing can considerably change, among others, the tree shape, allometry, and stem form factor, most studies and models to date use tables, factors and equations developed for monocultures and apply them to mixed-species stands. Individual tree structure and biomass analyses are needed that take the local environment into consideration and enable prediction of the tree and wood attributes accounting for tree size as well as the structural growth constellation of individual trees within the stand (i.e., neighbourhoods).

- Effects of structure.

It is still uncertain to what extent species identity and stand structural traits drive mixing effects such as overyielding, crown extension, or overdensity. Disentangling the effects of compositional and structural diversity in mixed, uneven-aged forests is relevant for both the advancement of theory and for the development of silvicultural approaches to mixed-species management. For this purpose long-term reference conditions (i.e., experiments that include unmanaged/unthinned plots) are needed, in addition to plots that exhibit various degrees of tree density and structural heterogeneity.

- Species combinations.



Most studies thus far have focused on the most relevant 2-species combinations (e.g., spruce-beech, oak-beech) while other important combinations such as pine-oak, larch-beech, fir-beech, or spruce-fir-beech and pine-beech-oak have received scant attention. We suggest installing new systematic experiments to quantify the mixing effects on tree and stand growth for a greater range of species combinations. To investigate underlying ecological or physiological principles guiding stand dynamics, we recommend that species combinations consider both potential species complementarity as well as combinations where no complementarity is expected. Further, traditional growth and yield studies that primarily focus on experiments, inventory data analyses, and modelling of 2-species mixtures in even-aged stands should be expanded to include mixtures with  $n > 2$  species, uneven-aged stand structures, and trees known to fix nitrogen as well as non-native (exotic) tree species.

- Scale of the experiments.

Mixing effects, morphological responses, stand structure, and species complementarity may all vary as a function of spatial scale. As a consequence, extents ranging from neighbourhood to stand to forest scales should be considered in experiments assessing these factors.

- Multiple ecological gradients (sites).

At this point, our concepts for predicting how different site conditions affect species interactions and potentially modify competition and/or facilitation within given species assemblages are tentative. New long-term experiments that yield recurrent inventory data, perhaps at fine spatio-temporal scales, could improve these concepts and contribute to a better understanding of the spatio-temporal changes of mixing effects in different species assemblages along multiple ecological gradients.

- Beyond productivity.

The majority of past studies has focused on mixing effects on stand productivity as quantified by mean annual growth or total yield. Further research is needed to investigate important additional yield components such as height, diameter, basal area, mortality, and regeneration.

- Wood quality.

Because mixed stands are projected to dominate future forests, it is essential to fill remaining gaps in knowledge about the effect of mixing on tree structure and wood quality (i.e., branchiness, specific density of wood, defects) (Pretzsch and Rais 2016). In the absence of

monetizing the provision of beneficial services such as clean water, infrastructure protection or the maintenance of biodiversity, economic opportunities in managed forest are largely constrained by the ability to produce high quality timber such as sawlogs or veneer (at least in Central Europe). It is imperative that scenario analyses and future silvicultural guidelines consider wood quality aspects that may be even more important for some landowners than potential productivity in terms of biomass or quantity, comparing wood quality produced in mixed versus pure stands.

- Risk assessment and trade-offs.

Given impending changes in climate trends, projected shifts in species distributions, and associated increased likelihoods of disturbance events such as more frequent and longer periods of drought or more intense windstorms, we suggest quantifying whether, and if so, how these risks might compare between variously mixed and monospecific stands. Consequently, the framework for interpreting the outcomes of future experiments, inventory data analyses and modelling of mixed forests should be expanded to include trade-offs and the potential for mixed stands and of various species assemblages to reduce the risk of catastrophic failures of forests and to improve the resiliency of forestry under expected climate change.

- Provision of ecological benefits and services.

Questions of growth and yield have largely dominated quantitative forest research during the first 200 years of scientific forestry and comparisons between mixed- and mono-specific stands thus far have largely focused on differences in productivity. Society is increasingly concerned with many other forest functions and services, however, notably water consumption, carbon sequestration and storage, non-timber forest products, and protection of human infrastructure against adverse effects of erosion. Thus, future decision-making will increasingly rely on analyses of trade-offs between the various functions that should be directly integrated and implemented in future models (Hynynen et al. 2005, Schmidt et al. 2006). Future scenario analyses could then provide policy-makers, planners, and decision-makers with an overview of the consequences of different management approaches, enabling forest managers to develop custom-made silvicultural prescriptions that most optimally meet the objectives of the landowner, perhaps even integrated into the larger, more complex landscape-level objectives regarding forest functions.

- Biological automation and treatment schedules.

The idea, that biological processes rather than silvicultural effort might be relied upon to guide successional dynamics and stand development, is slowly gaining traction in forestry. While biological automation might accommodate reduced resource inputs/effort into forest management operations, options for biological automation in mixed species management have largely remained unexplored. One such opportunity might be temporal mixtures of species, in which a subordinate species might be mixed with a dominant species to enhance growth opportunities for the latter. In this case, the subordinate species occupies growing space that will diminish over time in favour of the more competitive dominant species (e.g., oak – sycamore; Clatterbuck et al. 1987).

- Defining management success.

It is well known that rational management requires an unambiguous definition of objectives. Objectives can be “desired future conditions”, where multiple stakeholders agree on a target that is to be achieved, or may be the “avoidance of undesirable future conditions”, which might give managers more flexibility in decision-making (Zenner 2016). Although realistic management objectives are best formulated as an acceptable target range (e.g., Fig. 9), traditional silvicultural guidelines that recommend specific numbers of trees per hectare at different top heights post thinning typically aim at a single, narrow target (i.e., treatment that follows a guiding curve rather than a window/corridor of acceptable conditions). While a target corridor equips managers with a greater decision-space (i.e., more flexibility), this approach also allows managers to define management “success.” Future experiments should be planned to enable testing the feasibility of achieving different desired outcomes and/or staying within defined target corridors. Scenario modelling plays a critical role in helping managers define feasible outcomes and quantify the probabilities of achieving acceptable outcomes of mixed species management.

- Declining budgets.

The probability of achieving desired outcomes is not independent of the amount of silvicultural inputs/efforts. Silvicultural guidelines are often designed with very optimistic assumptions (i.e., many treatments entries, entries are done on time). However, given declining budgets, scenario analyses will need to explore the boundaries of species responses to decreasing inputs (i.e., decreasing spatio-temporal intensities of the application of silvicultural treatments) such that the desired outcomes can be achieved with the available resources. As a consequence, it will become increasingly important to link biological/

ecological scenario analyses to economic constraints and outcomes.

- Training opportunities.

Marteloscopes are a promising silviculture training tool for complex, mixed-species forest management (Bruciamacchie 2006, Schuck et al. 2015). Marteloscopes are stem-mapped plots in the field that are transferred and visualized in a computer or tablet. In the field, trainees can apply silvicultural treatments that are translated into virtual marking of trees in the computer. Currently available programs can immediately compute changes in mensurational variables (e.g., basal area, diameter distribution, standing volume) and, once linked with a dynamic individual-tree simulator such as SILVA (Pretzsch et al. 2002), might be able to predict and visualize likely effects of different silvicultural treatments or decision-making over time in mixed-forests. Thus, the main benefit of this educational and training approach is that participants can receive immediate visual feedback regarding changes in stand structures and stand dynamics, while also evaluating trade-offs in terms of wood quality, economic returns, habitat and nature conservation value.

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#### Authors’ contributions

HP initiated the review and drafted the manuscript. EKZ revised it critically for important intellectual content. HP and EKZ gave final approval of the version to be published.

#### Competing interests

Both authors declare that they have no competing interests.

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#### References

Ammer C (1996) Impact of ungulates on structure and dynamics of natural regeneration of mixed mountain forests in the Bavarian Alps. *For Ecol Manag* 88(1–2):43–53

- Ammer C, Bickel E, Kölling C (2008) Converting Norway spruce stands with beech—a review of arguments and techniques. *Aust J Forensic Sci* 125(1):3–26
- Amorosos MM, Turnblom EC (2006) Comparing productivity of pure and mixed Douglas-fir and western hemlock plantations in the Pacific Northwest. *Can J For Res* 36:1484–1496
- Assmann E (1970) *The principles of forest yield study*. Pergamon Press, Oxford
- Bauhus J, Forrester DI, Gardiner B, Jactel H, Vallejo R, Pretzsch H (2017a) Ecological Stability of Mixed-Species Forests. In: Pretzsch H, Forrester DI, Bauhus J (eds) *Mixed-species forests*. Springer, Berlin
- Bauhus J, Forrester DI, Pretzsch H, Felton A, Pyttel P, Benneter A (2017b) Silvicultural Options for Mixed-Species Stands. In: Pretzsch H, Forrester DI, Bauhus J (eds) *Mixed-species forests*. Springer, Berlin
- Bauhus J, Messier C (1999) Soil exploitation strategies of fine roots in different tree species of the southern boreal forest of eastern Canada. *Can J For Res* 29(2):260–273
- Bayer D, Seifert S, Pretzsch H (2013) Structural crown properties of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* [L.] in mixed versus pure stands revealed by terrestrial laser scanning. *Trees* 27(4):1035–1047
- Biber P, Borges JG, Moshhammer R, Barreiro S, Botequim B, Brodrechtova Y, Eriksson LO (2015) How sensitive are ecosystem services in European forest landscapes to silvicultural treatment? *Forests* 6(5):1666–1695
- Bielak K, Dudzinska M, Pretzsch H (2014) Mixed stands of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst) can be more productive than monocultures. Evidence from over 100 years of observation of long-term experiments. *For Syst* 23(3):573–589
- Binkley D, Kashian DM, Boyden S, Kaye MW, Bradford JB, Arthur MA, Fornwalt PJ, Ryna MG (2006) Patterns of growth dominance in forests of the Rocky Mountains, USA. *For Ecol Manag* 236(2):193–201
- Bruciamacchie M (2006) Le marteloscope, un outil pour apprendre la gestion durable – exemple d'évaluation de différents scénarios au marteloscope de Zittersheim (Vosges du Nord). In: Valauri D, André J, Dodelin B, Eynard M, Machel R, Rambaud D (eds) *Bois mort et à cavités – une clé pour des forêts vivantes*. Lavoisier, Paris
- Buongiorno J (2001) Generalization of Faustmanns formula for stochastic forest growth and prices with Markov decision process models. *For Sci* 47(4):466–474
- Buongiorno J, Michie BR (1980) A matrix model of uneven-aged forest management. *For Sci* 26(4):609–625
- Burkhardt HE, Tomé M (2012) *Modeling forest trees and stands*. Springer Science & Business Media, Dordrecht
- Burschel P, Huss J (1987) *Grundriß des Waldbaus*. Pareys Studentexte 49, Hamburg, Berlin
- Carnol M, Baeten L, Branquart E, Grégoire JC, Heughebaert A, Muys B, Verheyen K (2014) Ecosystem services of mixed species forest stands and monocultures: comparing practitioners' and scientists' perceptions with formal scientific knowledge. *Forestry* 87(5):639–653
- Clatterbuck WK, Oliver CD, Burkhardt EC (1987) The silvicultural potential of mixed stands of cherrybark oak and American sycamore: spacing is the key. *South J Appl For* 11:158–161
- Courbaud B, Goreaud F, Dreyfus P, Bonnet FR (2001) Evaluating thinning strategies using a tree distance dependent growth model: some examples based on the CAPSIS software "uneven-aged spruce forests" module. *For Ecol Manag* 145(1):15–28
- Dănescu A, Albrecht AT, Bauhus J (2016) Structural diversity promotes productivity of mixed, uneven-aged forests in southwestern Germany. *Oecologia* 182(2):319–333
- Eichhorn F (1902) *Ertragstafeln für die Weißtanne*. Verlag Julius Springer, Berlin
- Forrester DI (2014) The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. *For Ecol Manag* 312:282–292
- Forrester DI (2017) Ecological and Physiological Processes in Mixed Versus Monospecific Stands. In: Pretzsch H, Forrester DI, Bauhus J (eds) *Mixed-species forests*. Berlin: Springer.
- Forrester DI, Bauhus J, Cowie AL, Mitchell PA, Brockwell J (2007) Productivity of three young mixed-species plantations containing N<sub>2</sub>-fixing *Acacia* and non-N<sub>2</sub>-fixing *Eucalyptus* and *Pinus* trees in Southeastern Australia. *For Sci* 53(3):426–434
- Forrester DI, Bauhus J, Cowie AL, Vanclay JK (2006) Mixed-species plantations of *Eucalyptus* with nitrogen-fixing trees: a review. *For Ecol Manag* 233:211–230
- Forrester DI, Pretzsch H (2015) Tamm Review: On the strength of evidence when comparing ecosystem functions of mixtures with monocultures. *For Ecol Manag* 356:41–53
- Forrester DI, Tachauer IHH, Annighoefer P, Barbeito I, Pretzsch H, Ruiz-Peinado R, Stark H, Vacchiano G, Zlatanov T, Chakraborty T, Saha S, Sileshi GW (2017) Generalized biomass and leaf area allometric equations for European tree species incorporating stand structure, tree age and climate. *For Ecol Manag* 396:160–175
- Forrester DI, Tang X (2016) Analysing the spatial and temporal dynamics of species interactions in mixed-species forests and the effects of stand density using the 3-PG model. *Ecol Model* 319:233–254
- Gadow K (1996) Modelling growth in managed forests—realism and limits of lumping. *Sci Total Environ* 183(1–2):167–177
- Gadow K, Hui G (2001) *Modelling forest development* Vol. 57. Springer Science & Business Media, Dordrecht
- Gadow K, Zhang CY, Zhao XH (2009) Science-based forest design. *Math Comp For Nat Res Sci* 1(1):14
- Gaiser RN (1952) Root channels and roots in forest soils. *Soil Sci Soc Am J* 16(1):62–65
- Gayer K (1886) *Der gemischte Wald [The mixed forest]. Seine Begründung und Pflege, insbesondere durch Horst- und Gruppenwirtschaft*. Parey, Berlin
- Goisser M, Geppert U, Rötzer T, Paya A, Huber A, Kerner R, Bauerle T, Pretzsch H, Pritsch K, Häberle KH, Matyssek R, Grams TEE (2016) Does belowground interaction with *Fagus sylvatica* increase drought susceptibility of photosynthesis and stem growth in *Picea abies*? *For Ecol Manag* 375:268–278
- Greene DF, Zasada JC, Sirois L, Kneeshaw D, Morin H, Charron I, Simard MJ (1999) A review of the regeneration dynamics of North American boreal forest tree species. *Can J For Res* 29(6):824–839
- Grossiord C, Gessler A, Granier A, Pollastrini M, Bussotti F, Bonal D (2014a) Interspecific competition influences the response of oak transpiration to increasing drought stress in a mixed Mediterranean forest. *For Ecol Manag* 318:54–61
- Grossiord C, Granier A, Ratcliffe S, Bouriaud O, Bruelheide H, Češko E, Scherer-Lorenzen M (2014b) Tree diversity does not always improve resistance of forest ecosystems to drought. *Proc Natl Acad Sci* 111(41):14812–14815
- Hanewinkel M (2001) Economic aspects of the transformation from even-aged pure stands of Norway spruce to uneven-aged mixed stands of Norway spruce and beech. *For Ecol Manag* 151(1):181–193
- Hasenauer H, Kindermann G, Steinmetz P (2006) *The tree growth model MOSES 3.0*. In: Hasenauer H (ed) *Sustainable forest management*. Springer, Berlin, Heidelberg
- Hector A, Bagchi R (2007) Biodiversity and ecosystem multifunctionality. *Nature* 448:188–190
- Holvoet B, Muys B (2004) Sustainable forest management worldwide: a comparative assessment of standards. *Int For Rev* 6(2):99–122
- Hynynen J, Ahtikoski A, Siitonen J, Sievänen R, Liski J (2005) Applying the MOTTI simulator to analyse the effects of alternative management schedules on timber and non-timber production. *For Ecol Manag* 207(1):5–18
- Jensen M E, Everett R (1994) An overview of ecosystem management principles. In: Jensen ME, Bourgeron PS (eds), Vol II: *Ecosystem management: principles and applications*, Portland
- Juchheim J, Annighöfer P, Ammer C, Calders K, Raunonen P, Seidel D (2017) How management intensity and neighborhood composition affect the morphology of beech (*Fagus sylvatica* L.) trees. *Trees*, doi:10.1007/s00468-017-1581-z
- Jucker T, Bouriaud O, Coomes DA (2015) Crown plasticity enables trees to optimize canopy packing in mixed-species forests. *Funct Ecol* 29(8):1078–1086
- Kelty MJ (1992) Comparative productivity of monocultures and mixed stands. In: Kelty MJ, Larson BC, Oliver CD (eds) *The ecology and silviculture of mixed-species forests*. Kluwer Academic Publishers, Dordrecht
- Knapp E (1991) *Zur Wuchsleistung der Unterbaubuche im ungleichaltrigen Kiefern-Buchen-Mischbestand vor und nach ihrer Übernahme als Hauptbestand auf Standorten des nordostdeutschen Tieflandes*. Deutscher Verband Forstlicher Forschungsanstalten, Sektion Ertragskunde Jahrestagung, Treis-Karden
- Knoke T (2017) Economics of mixed forests. In: Pretzsch H, Forrester DI, Bauhus J (eds) *Mixed-species forests*. Springer, Berlin
- Knoke T, Ammer C, Stimm B, Mosandl R (2008) Admixing broadleaved to coniferous tree species: a review on yield, ecological stability and economics. *Eur J For Res* 127(2):89–101
- Kuuluvainen T (2009) Forest management and biodiversity conservation based on natural ecosystem dynamics in northern Europe: the complexity challenge. *Ambio* 38(6):309–315

- Lewis EG (1942) On the generation and growth of a population. *Sankhya* 6(1):93–96
- Liang J, Buongiorno J, Monserud RA (2006) WestProPlus: a stochastic spreadsheet program for the management of all-aged Douglas-fir/western hemlock forests in the Pacific Northwest. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland
- Liang J, Crowther TW, Picard N, Wiser S, Zhou M, Alberti G, Schulze E-D, McGuire AD, Bozzato F, Pretzsch H, de-Miguel S, Paquette A, Hérault B, Scherer-Lorenzen M, Barrett CB, Glick HB, Hengeveld GM, Nabuurs G-J, Pfautsch S, Viana H, Vitrans AC, Ammer C, Schall P, Verbyla D, Tchebakova N, Fischer M, Watson JV, HYH C, Lei X, Schelhaas M-J, Lu H, Gianelle D, Parfenova EI, Salas C, Lee E, Lee B, Kim HS, Bruelheide H, Coomes DA, Piotto D, Sunderland T, Schmid B, Gourlet-Fleury S, Sonké B, Tavani R, Zhu J, Brandl S, Vayreda J, Kitahara F, Searle EB, Neldner VJ, Ngugi MR, Baraloto C, Frizzera L, Balazy R, Oleksyn J, Zawila-Niedzwiecki T, Bouriaud O, Bussotti F, Finér L, Jaroszewicz B, Jucker T, Valladares F, Jagodzinski AM, Peri PL, Gonmadje C, Marthy W, O'Brien T, Martin EH, Marshall AR, Rovero F, Bitariho R, Niklaus PA, Alvarez-Loayza P, Chamuya N, Valencia R, Mortier F, Wortel V, Engone-Obiang NL, Ferreira LV, Odeke DE, Vasquez RM, Lewis SL, Reich PB (2016) Positive biodiversity-productivity relationship predominant in global forests. *Science* 354(6309). doi:10.1126/science.aaf8957
- Liang J, Picard N (2013) Matrix model of forest dynamics: An overview and outlook. *For Sci* 59(3):359–378
- Liang J, Zhou M, Tobin PC, McGuire AD, Reich PB (2015) Biodiversity influences plant productivity through niche-efficiency. *PNAS* 112(18):5738–5743
- Metz J, Annighöfer P, Schall P, Zimmermann J, Kahl T, Schulze E-D, Ammer C (2016) Site-adapted admixed tree species reduce drought susceptibility of mature European beech. *Glob Chang Biol* 22:903–920
- Metz J, Seidel D, Schall P, Scheffer D, Schulze ED, Ammer C (2013) Crown modeling by terrestrial laser scanning as an approach to assess the effect of aboveground intra- and interspecific competition on tree growth. *For Ecol Manag* 310:275–288
- Nagel J, Schmidt M (2006) The silvicultural decision support system BWINPro. In: Hasenauer H (ed) Sustainable Forest Management growth models for Europe. Springer, Berlin
- Newton PF (1997) Stand density management diagrams: Review of their development and utility in stand-level management planning. *For Ecol Manag* 98(3):251–265
- Oliver CD, Larson B (1996) *Forest Stand Dynamics*. Wiley, New York
- Oliver CD, O'Hara KL (2004) Effects of restoration at the stand level. In: Stanturf JA (ed) Restoration of boreal and temperate forests. CRC Press, New York
- Peck JE, Zenner EK, Brang P, Zingg A (2014) Tree size distribution and abundance explain structural complexity differentially within stands of even-aged and uneven-aged structure types. *Eur J For Res* 133(2):335–346
- Pretzsch H (2014) Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. *For Ecol Manag* 327:251–264
- Pretzsch H (2016) Ertragstafel-Korrekturfaktoren für Umwelt- und Mischungseffekte. *AFZ-Der Wald* 14:47–50
- Pretzsch H, Biber P (2016) Tree species mixing can increase maximum stand density. *Can J For Res* 46(10):1179–1193
- Pretzsch H, Biber P, Ďurský J (2002) The single tree-based stand simulator SILVA: construction, application and evaluation. *For Ecol Manag* 162(1):3–21
- Pretzsch H, Biber P, Uhl E, Dauber E (2015a) Long-term stand dynamics of managed spruce–fir–beech mountain forests in Central Europe: structure, productivity and regeneration success. *Forestry* 88(4):407–428
- Pretzsch H, Bielak K, Bruchwald A (2013) Species mixing and productivity of forests. Results from long-term experiments. German title: Mischung und Produktivität von Waldbeständen. Ergebnisse langfristiger ertragskundlicher Versuche. *Allg Forst- und Jagdztg* 184:177–196
- Pretzsch H, del Rio M, Schütze G, Ch A, Annighöfer P, Avdagic A, Barbeito I, Bielak K, Brazaitis G, Coll L, Drössler L, Fabrika M, Forrester DI, Kurylyak V, Löff M, Lombardi F, Matovic B, Mohren F, Motta R, den Ouden J, Pach M, Ponette Q, Skrzyszewski J, Sramek V, Sterba H, Svoboda M, Verheyen K, Zlatanov T, Bravo-Oviedo A (2016a) Mixing of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) enhances structural heterogeneity, and the effect increases with water availability. *For Ecol Manag* 373:149–166
- Pretzsch H, Forrester DI (2017) Stand dynamics of mixed-species stands compared with monocultures. In: Pretzsch H, Forrester DI, Bauhus J (eds) Mixed-species forests. Springer, Berlin
- Pretzsch H, Forrester DI, Bauhus J (eds) (2017) Mixed-species forests, ecology and management. Springer, Berlin
- Pretzsch H, Forrester DI, Rötzer T (2015b) Representation of species mixing in forest growth models. A review and perspective. *Ecol Model* 313:276–292
- Pretzsch H, Grote R, Reineking B, Rötzer T, Seifert S (2008) Models for forest ecosystem management: A European perspective. *Ann Bot* 101:1065–1087
- Pretzsch H, Block J, Dieler J, Dong PH, Kohnle U, Nagel J, Spellmann H, Zingg A (2010) Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. *Ann For Sci* 67:712.
- Pretzsch H, Rais A (2016) Wood quality in complex forests versus even-aged monocultures: review and perspectives. *Wood Sci Technol* 50(4):845–880
- Pretzsch H, Schütze G (2015) Effect of tree species mixing on the size structure, density, and yield of forest stands. *Eur J For Res* 135(1):1–22
- Pretzsch H, Schütze G, Biber P (2016b) Zum Einfluss der Baumartenmischung auf die Ertragskomponenten von Waldbeständen. *Allg Forst- und Jagdztg* 187(7/8):122–135
- Prieto I, Armas C, Pugnaire FI (2012) Water release through plant roots: new insights into its consequences at the plant and ecosystem level. *New Phytol* 193(4):830–841
- Puettmann KJ, Ammer C (2007) Trends in North American and European regeneration research under the ecosystem management paradigm. *Eur J For Res* 126(1):1–9
- Puettmann KJ, Wilson SM, Baker SC, Donoso PJ, Drössler L, Amente G, Putz FE (2015) Silvicultural alternatives to conventional even-aged forest management—what limits global adoption? *For Ecosyst* 2(1):8
- Puhe J (2003) Growth and development of the root system of Norway spruce (*Picea abies*) in forest stands—a review. *For Ecol Manag* 175(1):253–273
- Richards AE, Forrester DI, Bauhus J, Scherer-Lorenzen M (2010) The influence of mixed tree plantations on the nutrition of individual species: a review. *Tree Physiol* 30(9):1192–1208
- Roja A, Diéguez-Aranda U, Rodríguez-Soalleiro R, Gadow K (2005) Modelling silvicultural and economic alternatives for Scots pine (*Pinus sylvestris* L.) plantations in north-western Spain. *Forestry* 78(4):385–401
- Rötzer T, Seifert T, Pretzsch H (2009) Modelling above and below ground carbon dynamics in a mixed beech and spruce stand influenced by climate. *Eur J For Res* 128(2):171–182
- Scherer-Lorenzen M, Körner C, Schulze E-D (2005) Forest diversity and function. *Ecol Studies* vol 176. Springer, Berlin
- Schmidt M, Böckmann T, Nagel J (2006) The use of tree models for silvicultural decision making. In: Hasenauer H (ed) Sustainable Forest Management growth models for Europe. Springer, Berlin
- Schmithüsen F (2007) Multifunctional forestry practices as a land use strategy to meet increasing private and public demands in modern societies. *J For Sci* 53(6):290–298
- Schröpfer R, Utschig H, Zanker T (2009) Das Fichten-Konzept der BaySF. *LWF aktuell* 68:7
- Schuck A, Kraus D, Krumm F, Held A, Schmitt H (2015) Integrate+ Martelloscopes – Calibrating silvicultural decision making. Integrate+ Technical Paper No. 1
- Schütz JP (1997) *Sylviculture 2*. In: La gestion des forêts irrégulières et mélangées. Presses Polytechniques et Universitaires Romandes, Lausanne
- Stone EL, Kalisz PJ (1991) On the maximum extent of tree roots. *For Ecol Manag* 46(1–2):59–102
- Thurm EA, Biber P, Pretzsch H (2017) Stem growth is favored at expenses of root growth in mixed stands and humid conditions for Douglas-fir (*Pseudotsuga menziesii*) and European beech (*Fagus sylvatica*). *Trees* 31(1):349–365
- Thurnher C, Klopff M, Hasenauer H (2011) Forests in transition: a harvesting model for uneven-aged mixed species forests in Austria. *Forestry* 84(5):517–526
- Usher MB (1966) A matrix approach to the management of renewable resources, with special reference to selection forests. *J Appl Ecol* 3:355–367
- Utschig H, Neufanger M, Zanker T (2011) Das 100-Baum-Konzept als Einstieg für Durchforstungsregeln in Mischbeständen. *AFZ-Der Wald* 21:4–6
- Vallet P, Perot T (2016) Tree diversity effect on dominant height in temperate forest. *For Ecol Manag* 38:106–114
- Weiskittel AR, Hann DW, Kershaw JA Jr, Vanclay JK (2011) *Forest growth and yield modeling*. Wiley, Chichester
- Wellhausen K, Heym M, Pretzsch H (2017) Mischbestände aus Kiefer (*Pinus sylvestris* L.) und Fichte (*Picea abies* (KARST.) L.): Ökologie, Ertrag und waldbauliche Behandlung. *Allg Forst- und Jagdztg* 188(1/2):3–34
- Wiedemann E (1951) Ertragskundliche und waldbauliche Grundlagen der Forstwirtschaft. Sauerländer, Frankfurt am Main
- Zeide B (1985) Tolerance and self-tolerance of trees. *For Ecol Manag* 13:149–166
- Zeller L, Ammer C, Annighöfer P (2017) Tree ring wood density of Scots pine and European beech lower in mixed-species stands compared with monocultures. *For Ecol Manag* 400:363–374



- Zenner EK (2016) Managing Central Hardwood forests within the context of the historic range of variability (HRV): challenges and opportunities. In: Greenberg CH, Collins BS (eds) *Natural Disturbances and Historic range of Variation, Managing Forest Ecosystems* vol 32. Springer International, Switzerland
- Zenner EK, Heggenstaller DJ, Brose PH, Peck JE, Steiner KC (2012) Reconstructing the competitive dynamics of mixed-oak neighborhoods. *Can J For Res* 42:1714–1723
- Zenner EK, Lähde E, Laiho O (2011) Contrasting the temporal dynamics of stand structure in even- and uneven-sized *Picea abies* dominated stands. *Can J For Res* 41(2):289–299
- Zenner EK, Puettmann KJ (2008) Contrasting release approaches for a mixed paper birch (*Betula papyrifera*)/quaking aspen (*Populus tremuloides*) stand. *North J Appl For* 25(3):124–132
- Zenner EK, Puettmann KJ, Krueger JA (2005) Early growth and vigor response of naturally regenerated eastern white pine (*Pinus strobus* L.) to overstorey aspen density and pathological pruning. *North J Appl For* 22:27–34
- Zhang Y, Chen HYH (2015) Individual size inequality links forest diversity and above-ground biomass. *J Ecol* 103:1245–1252

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