Understanding the complexity of mixed forest functioning and management: advances and perspectives

1. Introduction

Forests represent the largest terrestrial ecosystems. They provide a multitude of ecosystem services that contribute to human well-being, from the production of wood for fuel or industry, to the provision of food, habitats for biodiversity and public amenities. However, perhaps even more important nowadays is their capacity to capture a considerable amount of carbon through the growth of trees, associated vegetation, and sequestrate it in the long term in forest soils or wood products. This is a major contribution to the mitigation of ongoing climate change, which threatens the integrity of natural ecosystems and more generally life on the planet. However, forest ecosystems are themselves subject to an accelerated increase in damage caused by climatic hazards. The trend towards increasing temperatures and drought, but also extreme events such as heat waves, increase the risk of windstorms and forest fires and trigger the development of outbreaks of insect pests, which lead to large scale tree mortality.

There is therefore a real urgency to seek to increase the capacity of forests to adapt to climate change while maintaining their role in mitigating these changes. There are not many options on the table to meet this difficult challenge, but they all involve a change in forest management. Some argue for replacing currently used tree species with species or provenances that are both productive and adapted to drought, including the use of non-native provenances or species, but caution is needed (e.g. Fady et al 2016). Such reforestation resources are not easy to identify and substitution change may not work. If the objective is to replace one species with another in tree monocultures, this may not be sufficient. Indeed, a growing number of studies and scientific publications provide evidence that pure stands are more vulnerable to biotic (Jactel et al 2021) and abiotic (Jactel et al 2017) hazards than mixed stands. In addition, there is considerable work that show that mixed forests may be more productive (e.g. Liang et al 2016, Jactel et al 2018, Pretzsch et al 2020), especially over the long term (Jucker et al 2014, Morin et al 2014; del Río et al 2017), and provide a larger portfolio of ecosystem functions and services (Gamfeldt et al 2013, van der Plas et al 2016) than pure forests.

But then why are mixed forest not more widely recommended? Although knowledge of the ecology of mixed forests has increased over the last few decades, this is probably because there are still major knowledge gaps and uncertainties, particularly with regard to their management and increased costs (Nichols et al 2006, Coll et al 2017). For example, it is still difficult to propose simple recommendations to forest managers concerning the choice of species to be combined in mixed forests, and then there is a lack of guidelines for good silvicultural practices in the long

term. This is mainly due to the complexity of interactions between tree species in mixed forests that depend on many factors such as species traits, interactions with environmental conditions and stand structure. This currently prevents the generalization of rules for predicting mixing effects.

A sustained effort is therefore still needed to decipher the mechanisms underlying tree species mixing effects and use this scientific knowledge to develop management and decision support tools for stakeholders. The aim of this special issue is to bring together the best that is currently being done in terms of research on the functioning and management of mixed forests. This issue contains 26 articles covering important and complementary topics from tree species interactions and stand productivity (6), mixed forests response to climate change (9), provision of ecosystem functions or services in tree mixtures (6) and mixed-species forest management (5).

2. Insights from the special issue

2.1 Tree species interactions and mixed stands productivity

Studies on species interaction effects on productivity of mixed stands from long-term experiments are rather scare, especially for slow-growing species. Mason et al (2021) presented the results of a 30 years old experiment comparing growth of *Picea sitchensis* Bong. Carr and *Pinus sylvestris* L. mixed stands with different species proportion. They showed the age-dependent impact of species proportion on overyielding, i.e. on greater productivity than the mean (weighted by species proportion) of component species productivities in their respective monospecific stands (Pretzsch & Forrester 2017, pp 126-132), highlighting the importance of regulating species proportion along the stand rotation. Maguire and Mainwaring (2021) reported the influence of initial spacing and mixing species on species dynamics and the stand productivity of conifer-conifer mixtures based on unique long-term mixed-species spacing trials. Overyielding was most often non-significant, but greater and significant for the narrowest spacing.

Ruiz-Peinado et al (2021) also found non-significant overyielding in mixtures of *Picea abies* (L.) Kars and *Pinus sylvestris* across Europe (Fig. 1b), although they detected changes in tree allometry and stand structure which may increase stand stability. Aldea et al (2021a) explored species interactions at tree level in the same *Picea abies* - *Pinus sylvestris* triplets. Using competition indices, they revealed the importance of species stratification on tree growth and found that species interactions were modulated by winter temperature and drought. Species stratification was also a relevant canopy structure characteristic in congers like *Pinus sylvestris* and *P. pinaster* Ait. mixed stands. Cattaneo et al (2020) examined the effect of species interactions on crown architecture in this pine mixture. *P. pinaster* crowns exhibited lower volume and an upwards displacement in mixed stands, while *P. silvestris* maintained longer crowns, indicating species complementary strategies to better occupy canopy space.

Bowman et al (2021) used data from long-term experiments in the Netherlands to calibrate and validate the 3PGmix model for mixed stands of *Pinus sylvestris* and *Quecus robur* L. with the aim to examine species interactions under varying soil and climate conditions. Although under

current conditions overyielding was mainly attributed to *Q. robur*, *P. sylvestris* competitiveness increased on poor sandy soils and under warmer and drier projected climate.

2.2   *Tree species response to climate*

Whether mixing species can improve tree resistance and resilience to drought events is still under debate, studies on this topic showing contrasting results (Grossiord 2019). Pardos et al (2021) analyzed resistance and resilience to drought in 30 triplets of pure and mixed stands involving eleven tree species, covering a large gradient from Mediterranean to hemiboreal forests. On average, mixed stands showed higher resistance and resilience to drought events than pure stands. The effect of mixing species was greater in conifer-broadleaved mixtures (Fig. 1c). However, the large variability in the results recall the complexity of this relationship. Jacobs et al (2021) found that *Fagus sylvatica* L. trees were more exposed to drought when admixed with *Quercus petraea* (Matt.) Liebl., due to greater growth rates and less conservative water use in mixtures, whereas *Q. petraea* was not influenced by admixed species. Serra-Maluquer et al (2021) investigated tree growth response to drought in *Abies alba,* under different neighborhood composition (intra- and inter-specific), and their relationship to soil biotic and abiotic characteristics. The found that fir growth response to drought depended on neighborhood species identity, where different soil microbial composition were observed.

Martin-Blangy et al (2021), who also used a triplet approach, compared *F. sylvatica* physiological response to drought in pure and mixed stands with *Abies alba* Mill. and *Quercus pubescens* Wild under different climatic conditions. They found no general pattern of mixing effects on water use efficiency and water uptake sources. Overall, *F. sylvatica* did not benefit from growing in these mixtures during dry periods. Based on the same triplets, Toïgo et al (2021) analyzed both stem and shoot growths during four years. Mixture effect was more often positive on branch growth than on stem growth, which suggest that considering only diameter growth can bias interpretations of diversity-productivity relationships.

Besides the species response during extreme drought events, other studies addressed how species interactions modify species sensitivity to climate. Nothdurf (2020) employed a hierarchical Bayesian model to analyze tree growth trends for different species growing in mixed and pure stands in Austria. He found species-specific growth trends that changed with elevation, but hardly any change between mixed and pure stands. Vospernik (2021) parametrized a basal area increment model for 22 tree species using data from Austrian National Forest Inventory, including explicitly climate variables and mixing effects. For most of species mixing effects were significant, but interactions which site or annual climate variables could not be identified.

Aldea et al (2021b) studied species intra-annual stem radial variation in dependence on weather conditions in mixed stands of *Pinus pinaster* and *Quercus pyrenaica* Wild to identify possible species niche complementarity. The two species showed general synchrony in intra-annual stem radial variation, but differences in the increment onset dates and in response to weather conditions, indicating some degree of temporal complementarity. Based on tree ring data from mixed mountain forests of *Picea abies-Abies alba-Fagus sylvatica*, del Río et al (2021) explored spatio-temporal patterns of intra- and inter-specific growth synchrony. Growth synchrony patterns were dependent on both climate and elevation. Inter-annual and log-term growth

variation was less synchronous between species than within species, suggesting niche complementarity at both temporal scales.

2.3   Other ecosystem functions in mixed forests

Biomass accretion is one of the most important functions in forest ecosystems as it derives benefits and goods such as carbon sequestration, timber and wood for energy. Although species mixtures increase biomass accumulation through a better light-used efficiency (Forrester et al. 2017, Gough et al. 2019), this does not imply a clearly better foliar nutrition in *Fagus sylvatica-Pinus sylvestris* mixtures (De Streel, 2021). Another plausible factor influencing biomass production is a competitive reduction for belowground resources due to root complementarity. However, Yeste et al. (2021) showed that fine root biomass of *Pinus sylvestris* trees was reduced in presence of *F. sylvatica* roots that dominated soil environment at different depths, pointing to competition among species (Fig. 3a).

Osei et al (2021) found that soil organic carbon (SOC) content was mainly driven by species identity rather than by mixing effects of *P. sylvestris, Q. robur* and *F. sylvatica*. Yeste et al. (2021) showed that SOC content significantly differed between soil depths but not between pure and mixed neighbourhood.

Krajnc et al (2021) analyzed the effect of species composition, bedrock and tree size on wood density in pure and mixed stands of sub-Mediterranean *Pinus nigra* Arnold and *Q. pubescens* in Central Europe. The mixture increased the wood density but to a lesser extent than the species identity, the crown social class or the soil site characteristics. The authors stressed the need to account for wood density and species proportion when converting growth measurements into carbon sequestration.

Biotic soil communities, like arthropods, are key drivers of important functions such as litter decomposition and turnover. Korboulewsky et al. (2021) confirmed that the addition of broadleaved species in coniferous forests can increase *Collembola* species richness in arthropods soil communities, which can improve litter decomposition and turnover. This was the case for lowland *P. sylvestris* and *A. alba* stands mixed with *Q. robur* and *F. sylvatica*, although the effect was not significant in mountain sites due to worse litter quality.

Calama et al (2021) tested the potential impact of climate change on the carbon sequestration, non-wood forest products yield, economic income and structural complexity in Mediterranean mixed forests of *Pinus pinea*, *Quercus ilex* and *Juniperus spp.* Using a modelling approach, they showed that the worsening of climatic conditions decreased the provision of ecosystem services in this type of forest, but the mixture mitigates the negative outcomes.

2.4   Forest management

One basic concept for designing thinning regimes is the density-growth relationship. Thurm and Pretzsch (2021) used data from 124 long-term plots to investigate this relationship in *Fagus sylvatica* L. mixed stands. They found a constant stand growth for a density range between the 70 and 100 % of maximum density, although the growth-density patterns varied with stand age and admixed species. Regarding thinning methods, their results indicate that weak thinnings from above can be recommended for maximizing growth in mixed beech stands.

Species height growth patterns determine mixed-species stand dynamics and therefore silvicultural decisions. Stimm et al (2021) demonstrated that height-growth patterns of *Quercus*

petraea and *Quercus robur* were strongly affected by site climate conditions, stand density and vertical structure of stands, being this influence lower in mixed stands. These results suggest that under climate change oak growth can be enhanced by silviculture measures.

Brzeziecki et al (2021) showed the utility and practicability of the demographic equilibrium approach to define specific silvicultural prescriptions adapted to complex stand structures. Its main limitation is the need for species-specific functions of ingrowth, tree growth and mortality.

Application of diameter-limit cuttings have been frequent in northeastern North America mixed hardwood-conifer forests, resulting in impoverished stands. Raymond et al (2020) compared the rehabilitation capacity of these forests under three regeneration methods and control treatment combined with 3 site preparation treatments. Although the unmanaged stands showed the highest resilience, shelterwood system combined with scarification can speed up rehabilitation. Maleki et al (2021) used the SORTIE-model (Coates et al 2003) to evaluate the long-term effect of clear-cuttings and different partial harvesting on mixed stands structure and species composition in western Canada. They found that spatial distribution had a greater effect than intensity of partial harvesting on stand dynamics.

3. Outlook

An important finding of most recent studies on the functioning of mixed forests, including those reported in this special issue, is that their performance is not related to the number of associated species, i.e. to tree species richness, but to their composition. In particular, it emerges that the functional contrast between species to be mixed would be a critical factor, notably because it underpins ecological niche complementarity, facilitation, and asynchrony of response to disturbances, which are some of the key mechanisms explaining the better performance of richer plant communities. A simple application of this finding is the common recommendation to combine conifers and broadleaves in mixed forests. However, as shown in this issue, species complementary in use of canopy space or temporal complementarity can also occur in conifer - conifer mixtures. Thus, we need to go beyond this first step in advising managers on the design of mixed forests, as they need more precision in the choice of coniferous or deciduous species. Further work should therefore focus on trying to identify the key functional traits, or more likely trait *syndromes*, that drive the functioning of individual species and more importantly their interactions when associated. Such a return to the fundamentals of functional ecology and community ecology could pave the way for a better capacity to identify the species to be associated in order to secure the proper functioning and maximize the performance of mixed forests.

Another important finding of recent years is that compositional diversity (e.g. identity of associated species) and structural diversity (e.g. diameter heterogeneity or height stratification) jointly drive mixed forest stand dynamics (Fig. 4d). An important consequence of this observation is that planting mixed species is often not enough and that it is then necessary to assist their coexistence with silvicultural interventions throughout the forestry cycle, especially when the associated species do not have the same growth rates and requirements. Questions as fundamental as the initial spacing, the species proportions, the intermingling pattern, the thinning regimes must therefore still be studied in depth in order to better develop guidelines for the sustainable management of mixed forests.

Although there is increasing evidence in the scientific literature that mixed forests perform some essential ecological functions better than tree monocultures, fewer studies verify that the same mixed forests optimally perform all of these functions simultaneously (Baeten et al 2019). In other words, the question of the multifunctionality of mixed forests remains open as trade-offs between ecological processes or functions often occur. It is often said that the management of forests is a matter of compromise, and this is probably even truer of mixed forests because they are by nature more complex. However, as multifunctionality is not often properly paid, the search for compromises between the different functions or services produced by mixed forests should not be left to forest managers alone. The cost of production and the income derived from all services must obviously also be factored into the equation. Here, more than anywhere else, the need for multidisciplinary and interdisciplinary research is apparent.

At the beginning of this editorial we asked the question of why there are so few mixed forests in production systems. A final key element in answering this question is undoubtedly the lack of communication. Pedagogy must be applied to forest managers to convince them of the merits and limitations of this type of forest. Tools, such as demonstration sites, are needed in this context. Nevertheless, beyond the managers, the whole society needs to be reached. The forestry sector must also be able to offer an outlet or a market for the companion tree species. Decision-makers must take this type of forest into consideration when it comes to program major restoration plans, especially in disturbed ecosystems. Finally, citizens must be informed that the extension of forested areas is necessary to mitigate climate change and, in this context, the species composition and structure of new plantation forests should be debated.

References

Baeten L, Bruelheide H, van der Plas F, et al. Identifying the tree species compositions that maximize ecosystem functioning in European forests. J Appl Ecol. 2019;56:733–744. https://doi.org/10.1111/1365-2664.13308

Coates KD, Canham CD, Beaudet M, Sachs DL, Messier C (2003) Use of a spatially explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forests. For Ecol Manage 186: 297–310. https://doi.org/10.1016/S0378-1127(03)00301-3

Coll L, Ameztegui A, Collet C , et al (2018) Knowledge gaps about mixed forests: What do European forest managers want to know and what answers can science provide? For Ecol Manage 407: 106-115. https://doi.org/10.1016/j.foreco.2017.10.055

del Río M, Pretzsch H, Ruíz-Peinado R et al (2017) Species interactions increase the temporal stability of community productivity in *Pinus sylvestris–Fagus sylvatica* mixtures across Europe. J Ecol 105: 1032-1043. https://doi.org/10.1111/1365-2745.12727

Fady B, Cottrell J, Ackzell L. et al. (2016) Forests and global change: what can genetics contribute to the major forest management and policy challenges of the twenty-first century?. Reg Environ Change 16: 927–939. https://doi.org/10.1007/s10113-015-0843-9

Forrester DI, Ammer C, Annighöfer PJ, et al (2017) Effects of crown architecture and stand structure on light absorption in mixed and monospecific Fagus sylvatica and *Pinus sylvestris* forests along a productivity and climate gradient through Europe. J Ecol 106: 746– 760. https://doi.org/10.1111/1365-2745.12803

Gamfeldt L, Snäll T, Bagchi R, et al (2013). Higher levels of multiple ecosystem services are found in forests with more tree species. Nature communications 4(1): 1-8. https://doi.org/10.1038/ncomms2328

Gough CM, Atkins JW, Fahey RT, Hardiman BS (2019) High rates of primary production in structurally complex forests. Ecology 100: 1–6. https://doi.org/10.1002/ecy.2864

Grossiord C (2020) Having the right neighbors: how tree species diversity modulates drought impacts on forests. New Phytol 228: 42-49. https://doi.org/10.1111/nph.15667

Jactel H, Bauhus J, Boberg J, et al (2017) Tree diversity drives forest stand resistance to natural disturbances. Current Forestry Reports 3(3): 223-243. https://doi.org/10.1007/s40725-017-0064-1

Jactel H, Gritti ES, Drössler L, Forrester DI, Mason WL, Morin X, Pretzsch H, Castagneyrol B (2018) Positive biodiversity-productivity relationships in forests: climate matters. Biol Lett 14(4):20170747. https://doi: 10.1098/rsbl.2017.0747.

Jactel H, Moreira X, Castagneyrol B (2021) Tree Diversity and Forest Resistance to Insect Pests: Patterns, Mechanisms, and Prospects. Annual Review of Entomology 66: 277-296. https://doi.org/10.1146/annurev-ento-041720-075234

Jucker T, Bouriaud O, Avacaritei D, Coomes D A (2014) Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. Ecology Letters 17(12): 1560-1569. https://doi.org/10.1111/ele.12382

Liang J, Crowther T W, Picard N, et al 2016 (2016) Positive biodiversity-productivity relationship predominant in global forests. Science 354(6309): 1–12. https://doi.org/10.1126/science.aaf8957

Morin X, Fahse L, de Mazancourt C, Scherer-Lorenzen M, Bugmann H (2014) Temporal stability in forest productivity increases with tree diversity due to asynchrony in species dynamics. Ecology letters 17(12): 1526-1535. https://doi.org/10.1111/ele.12357

Nichols JD, Bristow M, Vanclay JK (2006) Mixed-species plantations: prospects and challenges. For Ecol Manage 233: 383–390. https://doi.org/10.1016/j.foreco.2006.07.018

Pretzsch H, Forrester DI (2017) Stand Dynamics of Mixed-Species Stands Compared with Monocultures. In: Pretzsch H, Forrester D, Bauhus J (eds) Mixed-Species Forests. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-662-54553-9_4

Pretzsch H, Steckel M, Heym M, et al (2020) Stand growth and structure of mixed-species and monospecific stands of Scots pine (Pinus sylvestris L.) and oak (Q. robur L., Quercus petraea (MATT.) LIEBL.) analysed along a productivity gradient through Europe. Eur J Forest Res 139: 349–367. https://doi.org/10.1007/s10342-019-01233-y

Van der Plas F, Manning P, Allan E, et al (2016) Jack-of-all-trades effects drive biodiversity–ecosystem multifunctionality relationships in European forests. Nature communications 7(1): 1-11. https://doi.org/10.1038/ncomms11109

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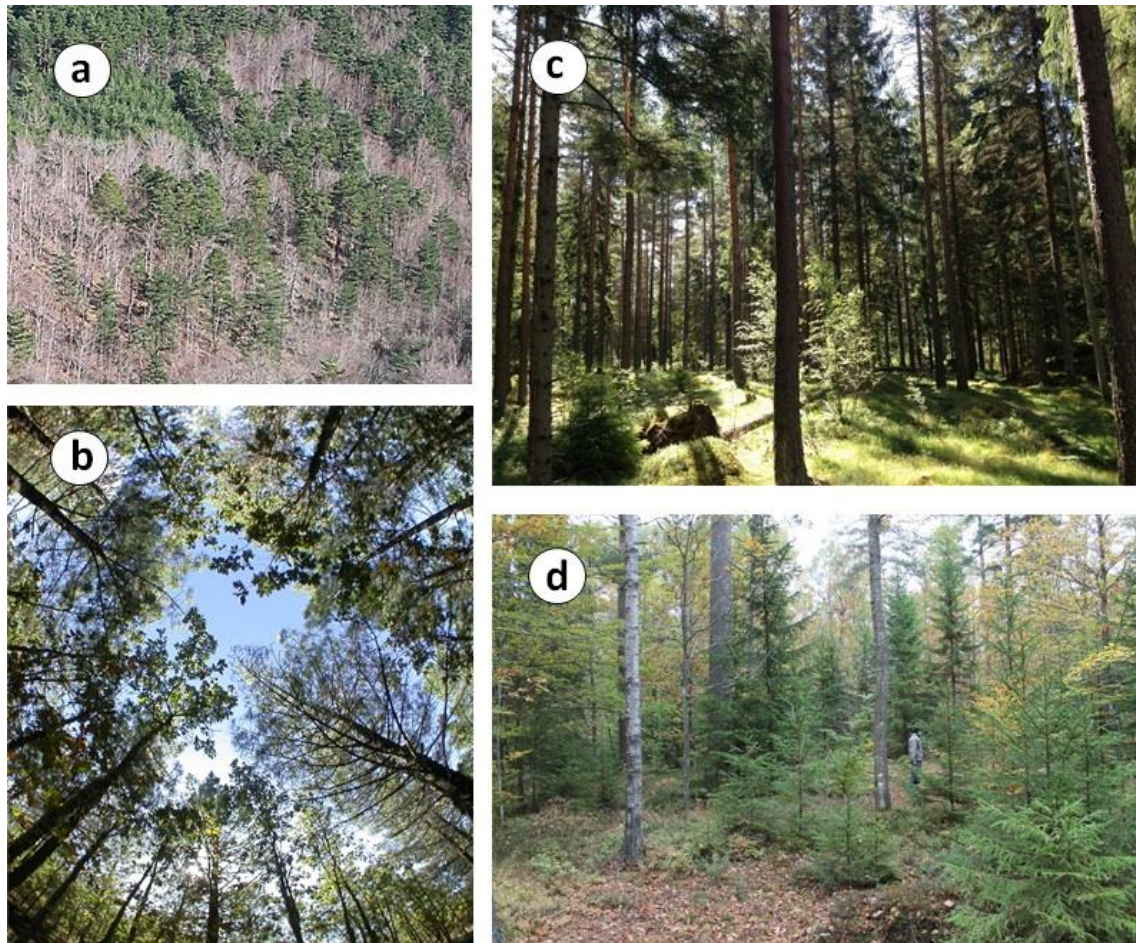
Fig. 1 Relevance of species traits and stand structure in mixed forest functioning:

a: Conifer-broadleaved mixtures with complementary aboveground traits, like *Pinus sylvestris* and *Fagus sylvatica*, can result in over-densities in comparison to monospecific stands (see Thurm and Pretzsch 2021). At belowground level, competition may be the predominant type of interaction between species (see Yeste et al 2021) (Photo: M. del Río)

b: Conifer-broadleaved mixed stands (photo: *Pinus pinaster-Quercus pyrenaica*) generally exhibit greater resistance and resilience to drought events than conifer-conifer mixtures (see Pardos et al 2021) (Photo: M. del Río)

c: Conifer-conifer mixtures, such as *Picea abies- P. sylvestris* stands, can also show complementary use of canopy space, which involve differences in stand structure and species growth between mixed and monospecific stands (see Aldea et al 2021, Mason et al 2021, Ruiz-Peinado et al 2021) (Photo: M. Löf)

d: Stands with multiple tree species (in this case *Betula pendula*, *F. sylvatica*, *P. abies*, *P. sylvestris*, *Populus tremula* and *Quercus petraea*) and structural diversity may be promoted and managed with selection systems to enhance forest functioning (Photo: J. Brunet)