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Knowledge gaps about mixed forests: what do European forest managers want to know and what answers can science provide?

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Abstract

Research into mixed-forests has increased substantially in the last decades but the extent to which the new knowledge generated meets practitioners' concerns and is adequately transmitted to them is unknown. Here we provide the current state of knowledge and future research directions with regards to 10 questions about mixed-forest functioning and management identified and selected by a range of European forest managers during an extensive participatory process. The set of 10 questions were the highest ranked questions from an online prioritization exercise involving 168 managers from 22 different European countries. In general, the topics of major concern for forest managers coincided with the ones that are at the heart of most research projects. They covered important issues related to the management of mixed forests and the role of mixtures for the stability of forests faced with environmental changes and the provision of ecosystem services to society. Our analysis showed that the current scientific knowledge about these questions was rather variable and particularly low for those related to the management of mixed forests over time and the associated costs. We also found that whereas most research projects have sought to evaluate whether mixed forests are more stable or provide more goods and services than monocultures, there is still little information on the underlying mechanisms and trade-offs behind these effects. Similarly, we identified a lack of knowledge on the spatio-temporal scales at which the effects of mixtures on the resistance and adaptability to environmental changes are operating. Our analysis may help researchers to identify what knowledge needs to be better transferred and to better design future research initiatives meeting practitioner's concerns.

Key-words: Species mixtures**,** review, forest management and functioning, participatory process, research challenges, ecosystem services, forest stability

1. Introduction

In recent years, the study of mixed forests has been the focus of increasing research efforts, in particular the consequences of admixing tree species for the productivity and stability of forest systems. This has generated a substantial amount of new knowledge (e.g. Pretzsch et al., 2013; Vilà et al., 2013; Morin et al., 2014; Tobner et al., 2016; Liang et al., 2016; van der Plas et al., 2016; among others), and the consolidation of important scientific initiatives and networks (Baeten et al., 2013; Bravo-Oviedo et al., 2014; Verheyen et al., 2016). From the research perspective, the recent advances in the understanding of mixed forests functioning are of unquestionable value, but the extent to which this information is responding to practitioners' concerns remains unknown.

We addressed this issue via a collaborative work in the context of the EuMIXFOR research network (Bravo-Oviedo et al., 2014) in which researchers from 30 different European countries participated. The study was divided into three steps. First, we conducted a Pan-European survey with the objective of identifying key questions related to mixtures that, from the perspective of forest managers, still require further research attention. Second, we ranked these questions by relevance according to the views of an independent set of European practitioners obtained via an online prioritization exercise. Finally, we evaluated current scientific knowledge for the highest ranked questions and we identified future research challenges in relation to them. The ultimate aim of our work was to reduce the commonly reported gap between knowledge generated from research and that required by forest managers (see Petrokofsky et al.,

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2010). In that respect, we expect our analysis will provide both (*i*) information to the research community on the priority knowledge needs of forest practitioners and (*ii*) brief reviews of the current state of knowledge regarding the topics of their concern. Finally, we expect that the identification of research challenges (based on the questions received from the practitioners) may help researchers to contextualise and design future research initiatives and may also facilitate the translation of new knowledge into practical outcomes.

2. Collection and prioritization of research questions by forest managers

2.1 Collection of questions

Each representative of the individual European countries that participated in the *EUMIXFOR* network contacted forest managers from that country who had expertise in the management of mixed-forests in either public or private ownership. We asked the managers to provide a list of the 5 – 10 key questions about mixtures for which they would like more information from the research community (preferably in the form of an interrogative sentence). Fifty-three forest managers from 15 countries responded to this request providing 289 questions (Fig. 1). The set of questions from each country was added sequentially to the pool of questions. The sets of questions brought by the last countries added to the list did not bring further information, suggesting that the main questions had already been gathered and that adding new countries would not increase the number of questions to be retained.

A multidisciplinary group of six experienced forest researchers (LC, CC, ML, BM, QP and KV) within the network classified each question into eleven broad themes (e.g. timber production, species interactions…) during a one-day workshop. Questions within each theme were then combined (when overlapping) and rephrased (if they were unclearly formulated or related to a very specific type of mixture) by this group of researchers. During this process, the only questions discarded were those that did not relate to mixtures. The process concluded with the formulation of 30 questions covering most of the replies originally received (Table S1).

2.2 Prioritization process

These 30 questions related to mixed forests were then ranked through an online prioritization survey conducted in 22 countries throughout Europe (Fig. 1). We contacted an independent sample of 168 forestry professionals (i.e. between 5 to 15 forest managers per country), working in different organisations (public institutions, private forests, forest associations) and with a professional interest in the management of mixtures. We presented the 30 questions (translated into their national language) to each of the 168 respondents that participated in the exercise, and we used the best-worst scaling (BWS) method to rank them according to the preferences of each individual.

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Fig. 1. Schematic representation of the participatory process conducted with European forest managers for the selection of the 10 questions used to structure the review. The countries colored in green corresponded to the ones that contributed to step 1 (above) and step 3 (below).

The BWS method (Finn and Louviere, 1992; Louviere et al., 2013) is a discrete choice task in which each respondent is asked repeatedly to choose the most important and the least important item from among randomly selected subsets of the original set of items, in this case of 4 out of the 30 questions. BWS forces respondents to discriminate among the presented alternatives, thus preventing some of the problems associated with other ranking methodologies, such as anchoring bias, i.e. the tendency of respondents to consistently use the middle points or one of the end points when using rating scales

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(Flynn et al., 2007; Rudd and Lawton, 2013). The prioritization exercise was conducted using an internet-based survey platform (SurveyGizmo, Boulder, CO, USA).

The values ascribed to the different questions ranged from nearly 63 for the highest ranked to about 39 for the lowest ranked questions (Table S1). A feature of the exercise was that a number of questions given an upper to middle ranking (e.g. ranks 8-18) received quite similar scores. In order to constrain the length of the review section that follows, we took an arbitrary decision to limit detailed discussion to the ten most highly ranked questions. Similar procedures of constraining results of participatory processes to the ten highest questions have been used in other studies (e.g. Petrovsky et al., 2010).

3. Revision of the current state of knowledge in relation to forest managers' questions

We synthesize below the current state of knowledge in relation to the ten highest ranked questions selected by forest managers. The questions were categorized into three broad groups as they refer to the relation between mixed forests and (*i*) stability, (*ii*) the provision of ecosystem services, and (*iii*) management. The questions within each group were addressed in the order we considered the most appropriate to facilitate the flow of writing and reading. In the sections below, the number in brackets next to each question shows its rank that resulted from the prioritization process (see Table S1).

3.1 Stability

- *Which mixtures of species provide the best resistance and best resilience to climate change and natural disturbances? (#1)*
- *Are mixed forests more resistant and resilient to climate change and natural disturbances? (#2)*

In recent years, the question of whether mixed forests are better able to cope with environmental change than monocultures has been a focus of attention (see for example the reviews by Thompson et al., 2009; Bauhus and Schmerbeck, 2010 or Scherer-Lorenzen, 2014). The concepts of resilience and resistance have been addressed and defined in many different ways (Brand, 2009). Here, we follow the approach of Hodgson et al., (2015) and we consider resilience to encompass both resistance and recovery; with the first being the capacity of the system to absorb an exogenous disturbance and the second its capacity to come back to an equilibrium after being disturbed (see also Oliver et al., 2015). Forest resilience can be approached at the level of periodic stresses (e.g. drought episodes) or of disturbances (e.g. windstorms, fires) (see Trumbore et al., 2015). In the case of most European forests, there is a large consensus that the impacts of both types of stressor are expected to increase with climate change (Seidl et al., 2011). The response of forests to periodic stresses relates to the concept of ecosystem stability, a concept that has been largely investigated in grassland ecosystems, where diversity helps to maintain the productivity of ecosystems subject to climate variations (Tilman et al., 2006; Isbell et al., 2015). The diversity-stability relationship in forest ecosystems is less clear (Thompson et al., 2009), although some comprehensive studies such as the ones by Morin et al., (2014) and Jucker et al., (2014) also reported more stable productivity of mixed-forests over time. Such stabilizing effects might be mediated by a reduction of the competition among species for growing resources (i.e. functional complementarity (Loreau and Hector, 2001)), asynchronic species-intrinsic responses to environmental fluctuations (Morin et al., 2014) or by temporal shifts in species interactions (i.e. temporal complementarity) (del Rio et al., 2017).

Forest resistance to biotic factors, such as insect herbivores or fungal pathogens, increases in mixed-forests which in general present lower pest abundance and experience lesser damage than monocultures (see meta-analysis by Jactel et al., 2005 or Haas et al., 2011). These findings are explained by different mechanisms such as reduced host tree density and accessibility ("associational resistance hypothesis", Barbosa et al., 2009), or by an increased presence of predators and parasitoids in more diverse forests (Guyot et al., 2016). However, reduced damage by insect herbivores in mixed forests is not observed consistently (see for example Vehviläinen et al., 2006; Schuldt et al., 2010; Haase et al., 2015) and the same occurs with fungal disease incidence (Nguyen et al., 2016). In some cases, reversed patterns (i.e. higher damage in mixed forests) have been reported when damages are triggered by generalist herbivores ("associational susceptibility hypothesis", Barbosa et al., 2009). Some authors have concluded that biotic damages are in many cases more related to the specific composition of the forests (or the type of herbivore) than to species richness *per se* (see meta-analysis by Vehviläinen et al., 2007 or Jactel and Brockeroff, 2007). Similar conclusions derive from the few existing studies investigating the impact of mammal herbivores in mixed stands (Vehviläinen and Koricheva, 2006, Metslaid et al., 2013).

Similarly to biotic damages, the role of tree diversity in the capacity of forests to resist severe abiotic disturbances (such as catastrophic windstorms or wildfires) is unclear and appears to be more dependent on structure and species combinations than on diversity (Dhôte, 2005; Grossiord et al., 2014; Pereira et al., 2014; Forrester et al., 2016, Metz et al, 2016). In contrast, tree diversity is generally considered to enhance the capacity of forests to recover from disturbances although this has been scarcely tested in field studies since it requires long-term monitoring and adequate information about the state of the forest prior to the disturbances. The higher resilience of mixtures to severe disturbances might be mediated by the higher diversity and higher redundancy of traits relevant to tree response to environmental changes (e.g. resprouting capacity, seed bank longevity) that these stands may present (Yachi and Loreau, 1999; Laliberté et al., 2010; Puettmann, 2011; Sánchez-Pinillos et al., 2016).

From a management perspective, promoting the coexistence of species belonging to different functional groups and/or with different strategies to face disturbances (to increase the probability of recovery processes) seems a good starting point (Sánchez-Pinillos et al., 2016). This mostly translates into trying to maintain the inherent complexity of forests, i.e. to develop (wherever possible) within- and among-stand heterogeneity in ecosystem structure, composition, and to accept variability in space and time as an inherent attribute to enhance forests' natural capacity to adapt and self-organize in response to gradual or abrupt environmental changes (Lloret et al., 2007; Puettmann et al., 2009; Messier et al., 2013).

3.2 Provision of ecosystem services

Forest ecosystem services are the range of benefits people obtain from forests. They include provisioning, regulating, cultural and supporting services (MEA 2005) and arise from ecosystem functions provided by organisms (Scherer-Lorenzen, 2014). Understanding the influence of biodiversity on ecosystem services requires analysing (*i*) the ecological processes that produce the ecosystem functions and (*ii*) the economic and sociological processes that value these functions into services that eventually provide human well-being (Butterfield et al., 2016).

Among forest ecosystem services, wood production has been the most studied service, but other services such as soil protection, plant and animal diversity, carbon sequestration and their relationship to tree diversity are currently being investigated in forest biomes.

- *How do mixed forests affect the quantity and quality of wood production? (#5)*

Several meta-analyses and reviews accounting for confounding factors such as site, species pool and stand characteristics, have shown an overall positive Diversity-Productivity Relationship (DPR) in forest ecosystems at stand/plot scale (typically <0.1 ha) (Paquette and Messier, 2011; Bauhus and Schmerbeck, 2010; Zhang et al., 2012; Liang et al., 2016). On average, stand production is higher in a mixture compared to expectation based on the mean production in pure stands of the component species, yet some individual monocultures may still be more productive than the most productive mixtures.

To value the wood volume produced and evaluate the socio-economic impact of tree diversity, it is necessary to sort the wood volume produced into wood quality classes, which correspond to particular classes of use and may be assigned a specific economic value. In a recent review, Pretzsch and Rais (2016) reported that the effects of tree diversity on wood quality were balanced and ambiguous, since tree morphology, structure and wood quality are strongly affected by stand structural heterogeneity, which is generally higher in a mixed than in a pure stand (see also Zeller et al., 2017).

- *Are mixed-forests more efficient in using resources (light, water, nutrients) than pure ones? (#10)*

Positive DPRs are related to selection (when changes in the relative yields of species in a mixture are non-randomly related to their yields in monoculture; Loreau and Hector, (2001)) and complementarity resulting from (*i*) competitive reduction (when competition is reduced in mixtures compared to pure stands) or (*ii*) facilitation (when a species improves the functioning of another species) (Vandermeer, 1989). Complementarity arises from inter-specific differences in physiology, phenology or morphology or from intra-specific differences that result from inter-specific interactions, and is affected by stand structure (Richards et al., 2010; Forrester and Bauhus, 2016). There is important variability among DPRs, even for a given species pool. The Monteith primary production model may be used as a framework to explain how the slope of the DPR changes along spatial or temporal gradients in resource availability or climatic conditions (Forrester and Bauhus, 2016). Complementarity is predicted to increase as the availability of a given resource declines (or as climatic conditions become harsher) if interactions among associated species result in an improvement of the availability, uptake or use-efficiency of that resource (or if interactions improve the climatic condition). Functional differences among admixed species appear to be a key condition for overyielding to occur (Zhang et al., 2012), but the net effect of these functional differences on overyielding depends on how they can reduce climate constraints / increase availability of limiting resources on a particular site.

- *Do mixed-forests provide more ecosystem services than monocultures? (#9)*

Carbon sequestration

The effects of tree species diversity on C sequestration may be assessed by considering (*i*) the biologically-mediated processes that drive the rates of C gain and loss and the size and longevity of C stocks, and (*ii*) the processes that determine the associated social and economic values (Diaz et al., 2009a; Diaz et al. 2009b). While the contribution of tree diversity to the net C uptake in aboveground tree components may be derived from DPRs, its impacts on belowground C storage, including roots and soils, remain much less documented (Hulvey et al., 2013). Because trade-offs at the individual tree species level prevent the maximizing of C sequestration across multiple C pools (e.g. root *vs* shoot biomass; Hulvey et al., 2013), maximizing forest C sequestration is expected to be achieved by using selected combinations of species traits. The complex effects of tree species diversity and identity on C storage are well illustrated when analysing soil C stocks. Dawud et al., (2016) observed a limited influence of tree species diversity and identity on the overall C soil storage (0-40 cm), but contrasting effects on the distribution of C within the soil profile. Diversity tended to increase C in deeper layers; by contrast, the effect of diversity on the forest floor C stock was inconsistent, in agreement with Handa et al. (2014) who clearly showed that the functional diversity of both decomposers and leaf litter, not simply litter species richness, promotes C and N cycling. As opposed to diversity, species identity tended to influence C storage in the upper forest floor layers. If confirmed by other studies, tree species diversity would therefore mainly benefit the longevity of C stocks through its effects on C storage in the deeper soil layers.

Plant and animal diversity

Canopy trees represent only a small part of forest biodiversity. The impacts of tree diversity on plant, animal and fungal diversity are complex. On one hand, mixed forests can be more productive, they also present higher structural heterogeneity which may provide more diverse above- and belowground microhabitats than monocultures, and may therefore host a greater number of organisms (De Deyn et al. 2004). On the other hand, neutral or negative effects of tree diversity may be observed in mixed forest where a dilution of each individual tree species may eliminate organisms that are dependent on particular tree species (Ampoorter et al., 2014; Tedersoo et al., 2016). In a literature review, Cavard et al., (2011) examined existing empirical evidence that tree mixtures promote the diversity of understory plants, songbird, soil fauna, and ectomycorrhiza in northern forests. They found no evidence of the existence of organisms uniquely associated with mixtures, species richness simply reflecting, at best, the accumulation of organisms associated with each canopy tree species. They also reported that tree diversity improves the diversity of understory plants (but see Barbier et al., 2008), avian and ectomycorrhizal communities (see also Bibby et al., 1989). Although many studies found positive effects of mixtures on earthworm or microarthropod diversity (see Korboulewsky et al., 2016), no general trend emerged on the relationship between mixed forests and soil fauna diversity.

Provision of multiple ecosystem services

Many studies have focused on the relationships between tree diversity and individual forest ecosystem functions, but very few studies have examined the impacts of tree diversity on ecosystem services, and even fewer studies have analysed multiple functions and services.

Multifunctional forest management requires that multiple ecosystem functions and services are simultaneously sustained. Several studies, mainly from grassland experiments, demonstrated that the level of biodiversity needed to maintain multiple functions was greater than the levels needed to maximize each individual function (Hector and Bagchi, 2007; Lefcheck et al., 2015); considering multiple locations and long time series in a changing environment further increases the needed level of biodiversity to provide multiple functions (Isbell et al., 2011).

The degree of multifunctionality of a forest can be determined by the number of ecosystem functions exceeding a predefined threshold value (Byrnes et al., 2014). Using such an approach, van der Plas et al., (2016) showed that multifunctionality increased with species richness for moderate levels of functioning, while it decreased when high function levels are desired. One may therefore conclude that the simultaneous maximisation of all functions at a stand level is not achievable as a result of trade-off between functions.

- *Which mixture of species (or functional groups) should be used to optimize specific or combined management targets (e.g. productivity, biodiversity, stability…)? (#4)*
- *Which positive and negative effects on different ecosystem functions (e.g. productivity, litter decomposition, stem quality) can occur when mixing particular species? (#6)*

Although many ecosystem functions are on average positively associated with canopy tree diversity (Nadrowski et al., 2010), there is often a considerable scattering around the mean, and for a given diversity level, the outcome of the interactions may be either positive, neutral or even negative, depending on the identities of the associated species (Scherer-Lorenzen, 2014). Moreover, even when similar species are combined, the outcome still depends on the set of current environmental conditions, including resource availability and climate constraints, as reported above for DPRs. From the manager's perspective, this means that effective tree species selection has to consider not only the functional differences between the investigated species for those traits involved in the function of interest, but also how functional diversity is expected to translate into positive effects given the environmental conditions at hand. While approaches using functional diversity metrics (Laliberté and Legendre, 2010; Mouchet et al., 2010) and empirical frameworks relating complementarity to resource availability and climate (Forrester and Bauhus, 2016) may assist optimal species selection, process-based models, such as those developed for growth (Forrester and Tang, 2016), appear quite promising as they combine the most relevant mechanisms and their interactions.

Regarding the optimization of combined management targets, van der Plas et al., (2016) showed that the relationship between multifunctionality and tree species richness described above was driven by the 'Jack-of-all-trades' effect, with only minor effects of either 'complementarity' or 'selection'. This means that whenever species effects on different functions are not perfectly correlated, the functioning of a multi-species mixture equals the biomass-weighted average of the function levels of monocultures of its component species.

For some functions, however, the relationship with tree species diversity remains much less documented or general patterns have not been discerned (Nadrowski et al., 2010). This is the case, among others, for those functions and processes that are more strongly affected by site conditions such as belowground processes and biogeochemical cycling (Scherer-Lorenzen, 2014). In addition to the identity effects discussed above, the possible context dependency of the Diversity Ecosystem functions Relationships

(DERs) could also explain the lack of net diversity effects when encompassing a range of sites, contrasting DERs slopes between sites being driven by environmental factors.

3.3 Management

- *What silvicultural treatments should be applied to maintain the desired species throughout the entire stand rotation? (#3)*

The silvicultural treatments applied to any mixture should reflect the management objectives chosen for the forest while respecting edaphic factors and species composition and characteristics. A useful framework for evaluating the potential effectiveness of silvicultural interventions at different phases of stand development is provided by a model of stand dynamics (Oliver and Larson, 1996) which separates stand development into four stages: stand initiation, stem exclusion, understorey reinitiation and old-growth (note that the last stage is rare in many managed forests). The creation of mixtures is best achieved in the first and third stages, whereas in the second stage thinning is used to ensure the survival of an existing mixture. However, at all stages, careful tending can be essential to ensure that the balance of a desired mixture is maintained.

During the stand initiation stage, acceptance of natural regeneration of a range of species that are suited to the site is often the best and most cost-effective way of developing a mixed stand. This approach can be combined with planting so that the regeneration forms the matrix between planted groups of a desired species (Saha et al., 2013), or can be favoured to create a two storied stand (Frivold and Groven, 1996; Stanturf et al., 2014). Two-storied mixed stands can also be created by deliberately underplanting fast growing pioneer tree species with slower growing and shade tolerant broadleaves or conifers (Pommerening and Murphy, 2004; Kelty, 2006; Paquette and Messier, 2013). Planting of mixtures is an option on nutrient poor soils where a more nutrient demanding species is mixed with one adapted to such sites, as is the case for the pine/spruce mixtures reported from the British Isles (Gabriel et al., 2005; Mason and Connolly, 2014) and Poland (Bielak et al., 2014) or where a nitrogen fixing species is mixed with another valuable timber species such as walnut (*Juglans regia* L.) or *Eucalyptus* spp. (Clark et al., 2008; Forrester et al., 2011; Radosevich et al., 2016).

Once the trees have closed canopy (stem exclusion), a period of intense inter-tree competition begins which can be mediated by the selective removal of individual trees or species (a.k.a 'thinning'). Where species are of compatible growth rates and shade tolerance, there is little need to adjust thinning strategies from practice in pure stands. The challenge occurs where the competition from one species can disadvantage the growth of a favoured species, as occurs with aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss) in boreal mixedwoods (Filipescu and Comeau, 2007). In such instances, thinning will need to favour stems of a more vulnerable but desirable species by removing immediate competitors. Other examples include mixtures of oak and more shade tolerant tree species (such as beech) where thinning is mandatory to prevent the latter outcompeting the more valuable oak (Hein and Dhôte, 2006; Johnson et al., 2009).

As the trees age, the canopy either begins to open up naturally or small gaps are created through final harvest. As a result, the increased light on the forest floor allows tree seedlings of a range of species to become established ('understorey reinitiation'). With control of ungulate browsing and careful tending, over time such seedlings (planted or naturally regenerated) can be promoted into the upper canopy layers and can be used to

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help convert a regular structure to an irregular one (Mosandl and Kleinert, 1998; Knoke and Plusczyk 2001; Nyland, 2003; O'Hara, 2014). This process can be used as a means of converting pure planted stands to mixed irregular forests, as in the conversion of Norway spruce to mixed conifer-broadleaved stands in some regions of central and western Europe (Spiecker et al., 2004; Ammer et al., 2008) or in restoring natural forest types after larch afforestation in northern China (Mason and Zhu, 2014). The development and formation of these mixed stands can be fostered by a range of irregular silvicultural systems (Matthews, 1991) involving combinations of tree species of different functional traits. While the general principles of the transformation process outlined above are well understood, their formulation into silvicultural guidelines for the management of particular species combinations in specific site conditions is often lacking. In part, this major knowledge gap reflects the historic emphasis given to experimentation with single species stands which means that the complexities of successfully manipulating species mixtures over time are poorly described and little known.

- *Do mixtures allow more flexibility and provide more options to adapt to changing management objectives than monocultures? (#8)*

Conceptually, the presence of more than one species in a maturing stand should give forest managers greater flexibility to adapt to changing objectives and to harvest different products at different stages of a stand's development (Nichols et al., 2006). However, it is difficult to find cases where this theoretical benefit has actually been realised or where there has been a comparison with pure stands. One example occurred in the UK in the 1960s when policy for public forests changed from developing a strategic supply of timber for the market to maximising the return on investment. As a result, a silvicultural regime for management of nursing mixtures of conifers and broadleaves in lowland Britain (Kerr et al., 1992) was changed from gradually removing the conifers to favour the broadleaves to one of eliminating the broadleaves to favour the faster growing conifers. The occurrence of aspen and white spruce in either two or single storey mixtures in boreal Canada is another example where the combination can allow managers to harvest either species for different products depending on market conditions and demand (Comeau et al., 2005).

- *How does the expected balance of benefits and costs compare between pure and mixed stands? (#7)*

For forest managers, any evaluation of benefits and costs from mixtures is heavily dependent on financial returns from wood production rather than involving consideration of wider aspects such as the relative delivery of ecosystems services (Quine et al., 2013). Establishment costs can heavily influence the potential profitability of mixtures. Saha et al. (2013), for example, showed that group plantings of oak in broadleaved regeneration were cheaper to establish and maintain than conventional pure oak planting in an analysis carried out in young (10-26 years old) forest stands of central and southern Germany. Comparisons of the relative returns from pure and mixed stands depend upon the anticipated yields from the two types of stands, and a situation where a high yielding species is mixed with a less productive one often results in lower total yield and a reduction in theoretical profits (Knoke et al., 2008). However, if the probability of risks from disturbances (biotic or abiotic), which are generally higher for pure stands, are calculated (e.g. Neuner et al., 2015) it can be shown that the mixed stand has a higher outturn, especially for a risk averse investor/owner and where longer rotations are incurred (Roessiger et al., 2013). In addition, a yield stimulus of 10%, depending on product and rotation length, can offset any increased costs associated with planting and managing mixed-species stands (Nichols et al., 2006). For example, if proper allowance is made for any positive yield improvement from growing species in mixture, then the financial performance of the mixture is better than that of the pure stand, as in two-storied mixtures of birch (*Betula pendula* Roth. and *Betula pubescens* Ehrh.) and Norway spruce (*Picea abies* (L.) Karsten) in Scandinavia (Valkonen and Valsta, 2001). However, such results can be influenced by stand structure since the financial outturn from single storied mixed stands of the same species was lower in the mixture than in the pure stand (Fahlvik et al., 2011). These results highlight how evaluation of the relative balance of the financial return from mixtures can be context dependent, influenced by factors such as forest type and owner objectives (Felton et al., 2016).

4. General discussion and future research directions

We summarise above the current state of knowledge in relation to the ten highest ranked questions related to mixed-forest management and functioning that are of major concern from the view of European forest managers. Our exercise could be conceived as a discussion between research suppliers and users: we consider that it has delivered results of high interest for both groups. The questions for which forest managers showed the most concern related to the capacity of mixed forests to respond to the effects of climate change and/or to the occurrence of natural disturbances. This could be explained by the recognized uncertainty of, and unpredictability associated with, these events and to the fact that they are not “controllable” by the implementation of any

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management strategy or action. Interestingly, these topics have been at the centre of many research initiatives (see Table 1). There is a general agreement in the scientific literature that mixtures are more resilient to natural disturbances than monocultures and that they present more options for adaptation to climate change. However, some of these positive aspects seem to be more related to the specific composition of the mixture than to tree diversity *per se* (see for example Metz et al., 2016), and additional efforts should be undertaken to assess which combination of species or functional groups needs to be promoted to tackle potential negative effects of predicted (or unexpected) environmental changes. Indeed, we share the view of Jactel et al. (2016) that further research efforts in this topic might be devoted to the understanding of potential trade-offs between species and communities with regards to the resistance and recovery to different disturbances and environmental changes. Improving our understanding of the spatio-temporal scales at which the effects of mixtures on the resistance and adaptability to change are operating might also be considered in future research projects (Table 1).

In contrast to the analysis of the underlying mechanisms behind the diversity – stability relationship, which has received substantial attention from the research community, we have poor information on how to manage tree mixtures over time and the cost (and benefits) behind these systems. Accordingly, we were able to provide very few evidence-based responses to the questions raised by the managers in relation to this area. Once the scarce published literature on this topic was reviewed, we observed that there is a critical lack of long-term research plots that explore and illustrate the silviculture of mixed forests in different forest types (Table 1). Such plots are necessary to validate the results of more theoretical studies as well as to support practice and the development of guidelines for the management of mixed forests. We also recognized there are almost no documented case studies which provide operational evidence of the greater management flexibility presumed to be provided by mixed forests, and very few integrated economic analysis showing the effects of a greater use of mixtures on the provision of ecosystem services within the forestry-wood chain. Such analyses may need to take proper account of uncertainty and risk and to provide costs and revenues which are relevant to managers' needs (Table 1).

Our survey also revealed the interest of forest managers in receiving research evidence about the widespread view that mixed forests provide more ecosystem functions and services than monocultures (five out of the ten highest ranked questions on mixed forests were related to this topic). The analysis we conducted confirmed this statement. Knowledge about tree species diversity effects on forest functioning has increased considerably in recent years resulting in general principles that could be translated into guidelines to be used by forest practitioners (Forrester and Bauhus, 2016).

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Table 1. List of the 10 high-ranked questions resulting from the participatory process with European managers. For each question the current level of scientific knowledge is evaluated as follows: + (hardly any research results available), ++ (individual case-studies available), +++ (integrative studies, reviews or meta-analyses available). Some key references and research needs are also provided.

[*] Refers to the level of knowledge on the relation between mixtures and the quantity of wood production. The existing knowledge in relation to the effects of mixtures on wood quality is much lower (+)

Rank-position	Question	Current knowledge	Some key references	Research needs
#1	Which mixtures of species provide the best resistance and best resilience to climate change and natural disturbances?	+	Pretzsch et al., (2013); Sánchez-Pinillos et al., (2016)	Role of different components of biodiversity (species richness, functional diversity) and organizational levels (e.g. trophic levels)
#2	Are mixed forests more resistant and resilient to climate change and natural disturbances?	+++	Jactel et al., (2005); Neuner et al., (2015)	Disturbance interactions and cascading effects; cross-scale approaches
#3	What silvicultural treatments should be applied to maintain the desired species throughout the entire stand rotation?	+	Pommerening and Murphy, (2004);	Establishment and analysis of long-term research plots
#4	Which mixture of species (or functional groups) should be used to optimize specific or combined management targets (e.g. productivity, biodiversity, stability…)?	++	Scherer Lorenzen, (2014); van der Plas et al., (2016)	Translation of individual and combined ecosystem functions into ecosystem services; long-term research plots
#5	How do mixed forests affect the quantity and quality of wood production?	+++[*]	Vilà et al., (2013); Pretzsch and Rais, (2016)	Factors behind transgressive overyielding of mixtures; effects of the mixture composition and stand structure
#6	Which positive and negative effects on different ecosystem functions (e.g. productivity, litter decomposition, stem quality) can occur when mixing particular species?	++	Nadrowski et al., (2010)	Impact of mixtures on belowground processes and biogeochemical cycles; interactions between belowground and aboveground responses; context dependency of the relationship between diversity and ecosystem functions
#7	How does the expected balance of benefits and costs compare between pure and mixed stands?	++	Knoke et al., (2008); Neuner et al., (2015)	Integrated economic analyses with inclusion of uncertainty and risk (timber price fluctuations, disturbance occurrence)
#8	Do mixtures allow more flexibility and provide more options to adapt to changing management objectives than monocultures?	+	---	Analyses of documented case studies; operational-scale demonstrations
#9	Do mixed-forests provide more ecosystem services than monocultures?	++	Gamfeldt et al., (2013)	Impact of mixtures on belowground processes and biogeochemical cycles
#10	Are mixed-forests more efficient in using resources (light, water, nutrients) than pure ones?	+++	Forrester, (2014); Forrester and Bauhus, (2016)	Development of process-based models for mixed stands;

However, we still lack integrated assessments of the role of the various components of biodiversity (e.g. species richness, species composition, community evenness, functional diversity, phylogenetic diversity) as well as of the organizational levels (trophic levels, taxa / organisms, …) on the provision of ecosystem functions (and in particular to those related to belowground processes and biogeochemical cycles) (Table 1). Indeed, we are still far from understanding how individual and combined ecosystem functions translate into ecosystem services. We also detected the need for further understanding of the biodiversity-ecosystem function relationship at all relevant temporal and spatial scales for management issues, while still accounting for confounding factors. Studies dealing with the response of forest ecosystem functions to biodiversity are often restricted to the stand scale (but see Chisholm et al., 2013), and to a very limited fraction of the stand cycle and tree lifespan. Lastly, we consider that additional efforts need to be devoted to the development of process-based models to help forest managers define best tree species combinations to optimize the supply of targeted services (while keeping the others at relatively high levels) (Table 1). For operational use, these models should provide managers with accurate information on product outturn, wood properties and timber value.

In conclusion, the results of our analysis show a general agreement between forest managers' concerns and the topics that are at the heart of most research projects dealing with mixed-forests. However, we have detected substantial differences in the amount of available knowledge relating to the various questions provided by the managers. Whereas most research projects have sought to evaluate whether mixed forests provide more goods and services than monocultures and are more stable when faced with environmental change (i.e. the *effects* of mixing, questions #2, #5), there is still little information about the underlying mechanisms and trade-offs behind these effects (although these questions are currently at the heart of a number of research initiatives (Verheyen et al., 2016)). Finally, our results stress the critical need of generating additional knowledge to provide forest managers with evidence-based silvicultural guidelines allowing the establishment and maintenance of mixtures over time under different environmental conditions.

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Supplementary information

Table S1. List of 30 questions ordered by their rank value (expressed on a 0–100 scale) after the prioritization exercise

	Question formulation	Rank-value
#1	Which mixtures of species provide the best resistance and best resilience to climate change and natural disturbances?	62,98
#2	Are mixed forests more resistant and resilient to climate change and natural disturbances?	58,88
#3	What silvicultural treatments should be applied to maintain the desired species throughout the entire stand rotation?	58,39
#4	Which mixture of species (or functional groups) should be used to optimize specific or combined management targets (e.g. productivity, biodiversity, stability…)?	58,21
#5	How do mixed forests affect the quantity and quality of wood production?	57,46
#6	Which positive and negative effects on different ecosystem functions (e.g. productivity, litter decomposition, stem quality) can occur when mixing particular species?	55,84
#7	How does the expected balance of benefits and costs compare between pure and mixed stands?	55,24
#8	Do mixtures allow more flexibility and provide more options to adapt to changing management objectives than monocultures?	53,84
#9	Do mixed-forests provide more ecosystem services than monocultures?	53,68
#10	Are mixed-forests more efficient in using resources (light, water, nutrients) than pure ones?	52,76
#11	How do effects of mixed-forest effects on productivity and resilience change along stand developmental stages?	52,49
#12	What stand structural and spatial patterns should be favoured to maintain mixtures of species with contrasting shade tolerance?	52,42
#13	What are the best options to convert monocultures to mixtures?	52,30
#14	How can the ecological impacts and benefits of mixed-forests be quantified?	52,01
#15	Are there adequate models to predict the growth and management of	51,51

	complex mixed stands?	
#16	Do intimate mixtures provide more (or different) benefits compared to patch or landscape scale mixtures?	50,57
#17	What are the most appropriate harvesting systems for use in mixed forests?	50,53
#18	Are there some site conditions that are more suitable for promoting tree species mixtures and for obtaining any associated benefits?	49,59
#19	What are the impacts of tree-species mixtures on soils at the stand and ecosystem levels?	48,20
#20	How much does biodiversity increase if we increase the number of tree species in the stand?	47,77
#21	How do we establish mixed species stands as part of afforestation programmes?	46,77
#22	Is there a minimum threshold in terms of species proportion required to induce a mixing effect at the stand level?	45,88
#23	Is it possible to predict the impacts of mixing on ecosystem- / stand-level properties based on the traits of the associated tree species?	45,54
#24	How do effects of mixed-forest on productivity and resilience change along abiotic gradients?	45,06
#25	Do we need improved sampling methods for use in inventories in mixed forests?	41,92
#26	Is there a desirable (optimal) balance to be achieved between the amount of pure and mixed stands at the landscape or regional level?	41,62
#27	What are the impacts of mixing on individual tree functioning (water status, nutrition)?	41,15
#28	Can any mixed species stands be sustained without management?	40,54
#29	Can the fragmentation characteristic of private forests lead to practical problems when managing mixed forests?	40,13
#30	What are the impacts of mixtures of provenances within tree species on ecosystem functioning (compared to those expected from mixtures of tree species)?	38,89