

European Mixed Forests: definition and research perspectives

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Abstract

Aim of study: We aim at (i) developing a reference definition of mixed forests in order to harmonize comparative research in mixed forests and (ii) briefly review the research perspectives in mixed forests.

Area of study: The definition is developed in Europe but can be tested worldwide.

Material and methods: Review of existent definitions of mixed forests based and literature review encompassing dynamics, management and economic valuation of mixed forests.

Main results: A mixed forest is defined as a forest unit, excluding linear formations, where at least two tree species coexist at any developmental stage, sharing common resources (light, water, and/or soil nutrients). The presence of each of the component species is normally quantified as a proportion of the number of stems or of basal area, although volume, biomass or canopy cover as well as proportions by occupied stand area may be used for specific objectives. A variety of structures and patterns of mixtures can occur, and the interactions between the component species and their relative proportions may change over time.

The research perspectives identified are (i) species interactions and responses to hazards, (ii) the concept of maximum density in mixed forests, (iii) conversion of monocultures to mixed-species forest and (iv) economic valuation of ecosystem services provided by mixed forests.

Research highlights: The definition is considered a high-level one which encompasses previous attempts to define mixed forests. Current fields of research indicate that gradient studies, experimental design approaches, and model simulations are key topics providing new research opportunities.

Key words: COST Action; EuMIXFOR; mixed-species forests; admixtures of species.

Introduction

European forests are a source of ecological services, goods, and socio-cultural benefits (Stenger *et al.* 2009). The estimated labour force in the forest sector was calculated in 2003 to be about 3.9 million people (Blombäck *et al.*, 2003). Current data showed that 2.6 million people are working in the whole sector in EU-27 (Forest Europe, UNECE & FAO, 2011). Despite this reduction, the forest sector continues to be an important driver for employment in rural areas, because forests provide wood raw material for construction, paper and fuel wood, supplementary food (berries, mushrooms, honey, etc...) and non-timber forest products (cork, resin, medicine plants etc.). Moreover, they contribute to capturing carbon emissions, to biodiversity enhancement and to the provision of recreational and aesthetic values in rural and peri-urban landscapes.

Mixed forests are an important source of ecosystem services. The “insurance hypothesis” suggests that their response to disturbance will be less intense and their recovery will be quicker than monocultures (Loreau *et al.*, 2001; Jactel *et al.*, 2009). Admixtures of species are more productive as long as species have differences in height pattern, phenology, crown and

root structure (Kelty, 1992; Morin *et al.*, 2011; Vilà *et al.*, 2013), provide more diverse goods and services and account for more structural and species diversity (Knoke *et al.*, 2008). This complexity in forest structure may foster self-regulation and provides higher adaptability to cope with increasing uncertainty due to climate change (Wagner *et al.*, 2014). Moreover, the gradual decrease in the area of single-species forests in Europe and a steady evolution towards mixtures of species (Forest Europe, UNECE & FAO, 2011).

The need for monitoring this portfolio of forest ecosystem services is acknowledged within the Pan-European region with the adoption of a framework of criteria and indicators of sustainable forest management (MCFPE, 2003). One of these indicators is tree species composition whose increase indicates the enhancement of biological diversity in forest ecosystems.

In 2010, EU-28 forests and other wooded land comprised 180.2 million ha (European Commission & EuroStat, 2013), which means 42.4% of its territory, and represents 4.5% of the world’s forests. For the whole of Europe the global share of forested land is 24.9% if the Russian Federation is included (FAO, 2011), and of this, 23% of land is covered by mixed forests in the pan-European region (Forest Europe, UNECE & FAO, 2011). It is worth noting that the figu-

res above for Europe quantify only the proportion of mixed broadleaved and coniferous woodland *sensu* TBFRA-2000 (FAO, 2000), *i.e.* forest land on which neither coniferous, nor broadleaved species account for more than 75% of the tree crown area. This type of mixed forest corresponds to the class G4 described by the EUNIS habitat type classification, characteristic of the transition zone between taiga and temperate lowland deciduous forests, and of the montane level of the major mountain ranges to the south (Davies *et al.*, 2004). However, such a definition of mixed forest is too narrow for Europe, where mixed forests of broadleaved species do naturally occur in the broadleaved deciduous forest zone (between the latitudes 40° N and 60° N) and mixtures of coniferous species are frequent in the subalpine region (*e.g.* *Larix* spp.-*Pinus cembra* forest, *Picea-Abies* forest).

This inconsistency clearly reveals a lack of consensus about mixed forest definition which may hinder the implementation of common policy measures regarding mixed forests aimed to enhance biodiversity, conservation, ecosystem services production, identification of job opportunities and comparison of research results.

In an attempt to standardize definitions applied in National Forest Inventories in Europe, Lanz *et al.* (2010) adopted the FAO's definition of 'forest' as an area covering more than 0.5 ha, with trees higher than 5 m that have a crown cover of more than 10%, or with trees able to reach these thresholds *in situ*. This definition excludes linear formations and agricultural and urban uses. However, the application of this forest definition is still challenging (Tomppo & Schadauer, 2012) and there is no similar definition or reference to mixed forests or a mixture of species.

In a global change context a common or harmonized definition is needed in order to properly compare present and future system behaviors. Harmonization is a two step procedure in which a reference definition is constructed and subsequently adjusted according to national definitions (Tomppo & Schadauer, 2012).

Available forest classifications do not allow for a straightforward identification of classes of mixed forests in Europe. As a matter of fact, all the 14 categories of the European Forest Types (EFTs) classification system (EEA, 2006; Barbati *et al.*, 2007) may include forest stands composed by several tree species. Barbati *et al.* (2014), processing National Forest Inventory (NFI) data from a sample of 10 EU countries, found that the share of single-species stands out of total

area covered by a given EFT at country level has a wide range of variability (15-100%) in categories which are species-poor (*e.g.* high latitude and altitudes Boreal or Alpine coniferous forests) and does not exceed 30% in species rich EFTs (*e.g.* Mesophytic and Thermophilous deciduous forests). This reflects a variety of patterns of multi-species stands across Europe. Multi-species stands are found in the early development phases of forest succession in the boreal forest zone (*e.g.* admixtures of spruce or pine with birch species), as well as in the late stages (*e.g.* admixtures of beech, fir and spruce in the mountainous vegetation belt, mixtures of broadleaved deciduous species), but might also be the result of the deliberate conversion of single-species monocultures (*e.g.* coniferous plantations established in the broadleaved deciduous forest vegetation zone). Accordingly, there is a need to develop a comprehensive definition able to take into account the wide range of patterns of occurrence of mixed forests in Europe.

In the EU context, forestry is an integral part of rural development and maintenance and improvement of forest stability is supported (Council of the European Union, 1999). The new EU forest strategy (European Commission, 2013) recommends that Member States make use of investments to improve the resilience, environmental value and mitigation potential of forest ecosystems to achieve nature and biodiversity objective as well as adapting to climate change (Kolström *et al.*, 2011). The timely identification of the role mixed forests can play in all these issues may have a strong economic impact for both public and private owners. The focus of the scientific community, stakeholders and final users is now more than ever concentrated in mixed forests.

Such an interest in mixed forests stimulated researchers from 30 European countries and 10 institutions from other 7 countries (Fig. 1) to combine in a network supported by a COST Action framework structured in three working groups (Table 1). The overall aims of this action are to:

- provide a sound overview of the role that mixed forests can play in the provision of environmental services in each of the following European bioregions: Boreal, Atlantic temperate, Continental temperate, Mountainous and Mediterranean. The overview would include a comparison with other regions worldwide;

- address how mixed forests can assist rural, peri-urban and urban communities to deal with environmental challenges, analyzing barriers to adaptive change, threats and opportunities;

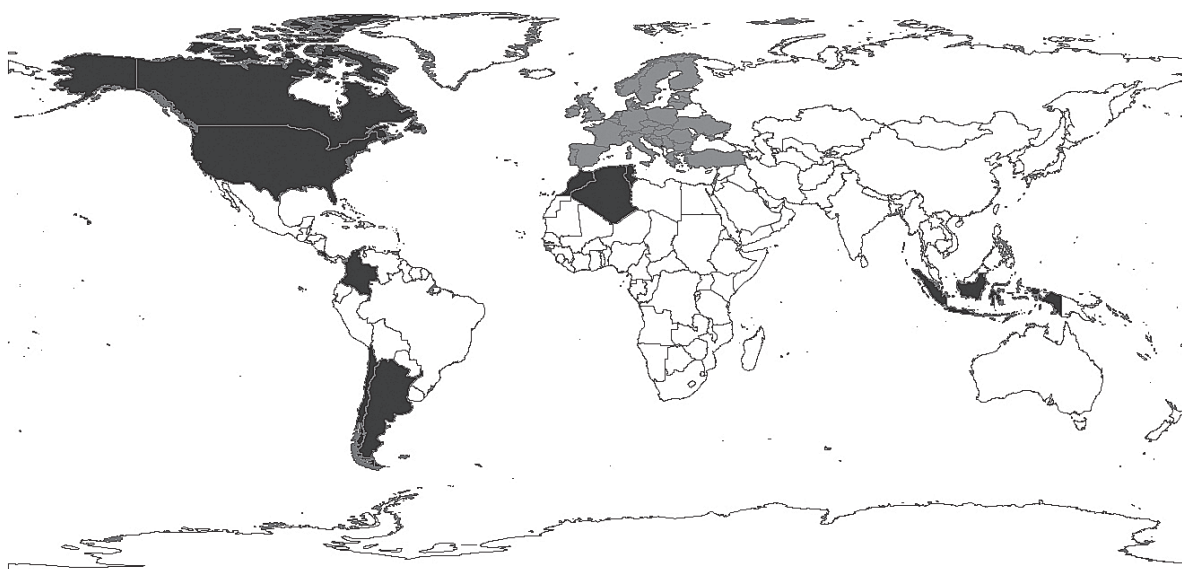


Figure 1. Participant countries in EuMIXFOR network. Light grey are COST Countries. Dark grey are international partners. A complete list of COST countries can be found at www.cost.eu.

Table 1. EuMIXFOR Working group structure and expected outputs

Working group	Objectives	Main expected output
WG1. Mixed forest functioning and dynamics	Analysis of impacts of the different components of global change on mixed forest (stability, biodiversity and ecosystem services)	Identification of experimental and observational platforms for analysis mixed forest functioning Identification of mechanisms driving interspecies interactions
	Identification of Gaps and research opportunities	Collaborative research work on mixed forest functioning
WG2. Adaptive forest management in mixed forest	Analysis of forest management practices in mixed forest	Identification of sustainable forest management practices.
	Identify models and DSS to promote and maintain mixed forest	Compilation of management tools applied to mixed forests
	Identification of “good practices”	Guidelines for sustainable forest management of mixed forests
WG3. Policy and social impact of mixed forests	Identify social impact of mixed forests	Analysis of user's preferences on ecosystem goods and services provided by mixed forests
	Identify policy measures to enhance job opportunities	Valuation of ecosystems goods and services provided by mixed forests
	Economic valuation of mixed forests	Strengthening liaisons between science, forest managers and policy-makers

- identify silvicultural practices and decision tools (e.g. decision support systems) for the creation and sustainable management of heterogeneous forests,

- establish different measures, such as standard protocols, common methodological approaches and experimental designs to create a research network in the public domain, to exchange results of research conducted in mixed forests, and the dissemination of their main results, accessible to policy makers, managers/owners and users.

Despite this background, however, the aspirations of this network can be hampered by the lack of a consistent definition as to the meaning mixed forests. In forest management planning, conservation measures or silvicultural prescriptions that are designed to fulfill an objective require the identification of target species, characterization of site features, and analysis of stocking degree and forest structure. Once a successful management approach is identified, it is usually applied in the same or analogous forest situations. An analogous forest means one that has the same or similar species, objectives and site conditions. However, in the case of mixed forests, adoption of successful management rules may not be straightforward as similarity among mixtures is difficult to achieve (*i.e.* similar species composition sharing, spatial pattern, functional relationship etc...). Therefore, adaptation of silvicultural practices to local conditions and designing new ones for complex forests, like admixtures of species, instead of adoption of current practices is gaining attention (Puettmann *et al.*, 2009). This task would be easier to achieve with a common definition of what practitioners and users understand by ‘mixed forest’

The main objective of this paper is to provide a reference definition of mixed forests. For that purpose, we summarize different approaches used to define mixed forests and discuss the current research topics that are being undertaken by the research community in these ecosystems. This definition may help to harmonize the calculation of mixed forest area and to consistently compare results of the main topics currently studied in mixed forests.

Definition approaches

Compositional approach

The starting point for defining a mixed forest is the trivial fact that a given forest or stand must be composed

of at least two tree species. However, it follows that the proportion of species on the basis of composition can differ depending on the species involved. Toumey and Korstian (1947) defined pure stands as those where 80 percent or more of the overstorey is of a single species. However, even if less than 10 percent in the overstorey is of a commercially or silviculturally valuable species the stand is classified as mixed. Depending on the contributing species, the ratio between species in mixed stands may differ greatly. Moreover, for a given mixed stand the description of its composition might vary depending on the species proportion definition used and, consequently, deriving different forest classifications.

In the most recent attempt to define mixed forests in western Europe, Bartelink & Olsthoorn (1999) extended the compositional definition by including a reference to spatial scale and species interaction: ‘stands composed of different tree species, mixed on a small scale, leading to competition between trees of different species as a main factor influencing growth and management’. However, the definition does not provide information about what “small scale” actually means. Moreover, other interactions between species occur in mixed forests, like facilitation (Forrester, 2014) or neutralism (Larocque *et al.*, 2013) and they seem to be excluded from this definition.

When describing the structure of a mixed stand it is not enough to give the species proportion, because the horizontal and vertical spatial patterns of the mixture can differ greatly between two stands with similar species proportions. When using variables expressing space occupancy for estimating species proportion it is important to consider that each species has different growing space requirements and different area potentially available. This is the idea behind the species proportion by area (Río & Sterba, 2009) calculated as a function of maximum or potential basal area for the species found in the mixture (Sterba, 1987). This method provides the maximum basal area for a given dominant height and it is compatible with Reineke’s self-thinning line.

Structural approach

Leikola (1999) presented a classification of mixed forest based on Langhammer (1971) that implicitly gives a definition of mixed forests based on form, type and grade of mixtures. The *form* is related to horizontal pattern of trees in a stand which can be by individual

stems, by row or by group; the *type* refers to the vertical distribution of trees in single- or multi-storied stands indicating that ‘in the strict sense’ only trees belonging to the same storey build up a mixed forest. The kinds of structures described as stratified mixtures by Smith *et al.* 1997 should be admissible under this definition, provided the strata are organized within the same storey. Finally the *grade* refers to the number and amount of tree species in a stand (compositional approach). However, while this classification system may help in identifying analogous mixtures it is not a definition by itself.

Developmental approach

Forest dynamics is a result of factors like disturbance regime, environmental gradients or species composition (Spies, 1997). In existing models of stand dynamics there are two repeated concepts where admixtures of species can be found: transition and stratification.

The idea of transition appears in late developmental phases (transition phase according to Spies (1997) and understorey reinitiation stage according to Oliver & Larson, 1990) where changes in species composition and structure occur. However, for both compositional and structural definitions of mixed forests this transition or temporal aspect of mixture is not taken into account.

For management purposes, canopy stratification is a core concept of mixed forest silviculture that operates at the stem-exclusion and understorey reinitiation developmental phase (Oliver & Larson, 1990). Smith *et al.* (1997) classified mixed forests into (i) single-cohort stratified mixtures, (ii) mixed, multi-cohort stands and (iii) mixed single-canopied stands. The former case develops from natural regeneration after a major disturbance or from a planned plantation. The second type of mixed forest proposed is found in undisturbed old-growth stands and although the stands may follow an irregular uneven-aged distribution they never approach a theoretical balanced J-shaped curve which, for these authors, was a result of silvicultural actions rather than a natural random processes (Smith *et al.* 1997). Finally, mixed single-canopied stands are defined as consisting of two species growing in height at the same rate. This kind of mixed stand is not common in forests and when it occurs it is a temporary situation that lasts until one species overtops the other.

Functional approach

All the previous approaches share common attributes: developmental definitions contain structural and compositional elements while structural definitions include compositional features. Consequently, irrespective of compositional, structural or developmental stages, the term ‘mixed’ is always used when at least two species co-occur in the same defined area. This confers tree species richness a pre-eminent role in the definition. However, there is a certain functionality limit in the definition of mixed forests as species co-occurrence or tree species richness. The reason is that more species might not necessary mean more functional differentiation. Oliver & Larson (1990) indicate that species with similar growth patterns (*e.g.* *Pinus taeda* and *Pinus palustris* in US) can interact as a single species. Such behavior is known in ecology as functional redundancy (de Bello *et al.*, 2007) which might be one possible mechanism explaining the lack of a strong biodiversity effect on productivity in some studies (Paquette & Messier, 2011). It is difficult to include this ecosystem functioning point of view in a definition because the mechanisms that affect tree species richness or biodiversity-ecosystem functioning relationships (B-EF) differ from site to site and as a stand develops or climatic conditions change. For example, complementarity resulting from interactions that influence soil resources often increase as the availability of those soil resources decreases (Forrester, 2014). In contrast, complementarity resulting from interactions that improve light absorption may increase as growing conditions improve (Forrester, 2014; Forrester & Albrecht, 2014).

A functional assessment of a mixed forest needs to take into account tree functional groups based on different criteria (Körner, 2005). Some examples are successional stage, the shade tolerance, crown architecture, litter quality or maximum rooting depth. However, these criteria are variable (even for the same species), they are often hard to measure, and functional traits’ richness instead of species richness should be preferred to define ecosystem processes (Scherer-Lorenzen *et al.*, 2005).

National Forest Inventory definitions

The increasing interest in the assessment of forest resources has improved the harmonization of NFIs

across Europe (Tomppo *et al.* 2010) especially concerning tree-related variables (Corona *et al.*, 2011). However, there is not a harmonized definition for mixed forests. There are three kinds of approaches in NFIs to deal with mixed forests.

- No definition: A simple list giving species' names and their measurements is recorded.
- Percentage canopy cover definition.
- Definitions based on forest characteristics other than canopy cover.

When no definition is provided (Poland, Italy) a species group classification is used instead (*e.g.* in Italy a mixed forest stand with 25% *Pinus halepensis*, 25% *P. pinea*, 25% *P. pinaster*, 25% *Quercus ilex* is assigned to the category of forest dominated by Mediterranean pines, as the pine coverage is 75%). Although definitions based on the percentage of canopy cover and other characteristics seem to be easy to compare across countries the reality is complex. In the case of percentage canopy cover, a percentage threshold is required as well as the size of the plot. It is evident that the larger the plot the more species will occur per plot. Austria's standard is 300 m² and 80-20% of cover sharing, Ireland uses the same minimum cover but the plot area is larger (500 m²). France expands the minimum area to approximate 2,000 m² and 75-25% sharing and Spain uses the same plot surface as France but the minimum cover for a species is 30%. There are NFIs that do not specify the minimum plot surface and only give minimum occupancy of canopy cover for one of the existing species (United Kingdom: 20%; Lithuania: 15%; Portugal: 25%; Norway: 30% in young stands). In the Dutch NFI, there is even a variable plot scale, to include at least 20 trees, of plots ranging from 78.5-156 m².

In the definition based on forest characteristics other than canopy cover, the difficulty of comparison is even greater as there are different measures or estimates used such as volume (Bulgaria, Finland, Norway in older stands, Turkey, Serbia), basal area (Belgium, Slovakia, Switzerland, Sweden) or number of stems per hectare (Sweden if trees are smaller than 7 m height) and their subsequent thresholds for each variable. This difficulty can be exacerbated because volume is not defined in the same way (total volume, stem volume or commercial volume) and basal area is even measured at different stem heights (1.3 or 1.5 m). The minimum diameter or circumference inventoried is another variable to take into account. It is clear that the number of species or grade (Langhammer, 1971) is the preferred discrimination rule of mixed forests in national inventory definitions.

Do spatial and temporal scales matter?

All the above definitions and approaches neglect the fact that the key concept of stand in forest management can prove inadequate when used to describe mixed forests. Forest management is commonly applied in small units, typically called a stand. Puettmann *et al.* (2009) list different influences on the development of stands as managing units and note that ecology only plays a tangential role in that process. A stand has been defined as 'a well-demarcated portion of woodland having a uniform structure and sufficiently limited in extent to permit a certain thinning treatment to be independently applied' (Assmann, 1970) or as 'a group of trees relatively homogeneous in age, structure, composition and site conditions' (Smith *et al.*, 1997). These definitions produce different outcomes in terms of mixed forest area. For example, in a two species mixture where the pattern of mixing is on a stem by stem basis and both species are present in equal proportions (consorting) both definitions can classify the same area (or group of trees) as mixed. However, if one of the species is present in a lesser proportion and overtopped by another (concomitant), the definition provided by Assmann would classify the stand as mixed as long as the area was sufficiently limited to apply a thinning treatment, whereas the definition provided by Smith might classify it as mixed depending on the degree of 'homogeneity of composition' in the group of trees. On the contrary, if the pattern of mixture is by group, Assmann's definition would classify such a stand as mixed if groups are located within the extension, whereas Smith's definition would classify it as mixed if the group of trees comprises all groups presented. A definition based on area rather than on groups of trees will produce more mixed forests. But, how large is 'sufficiently limited in extent'? If this cannot be defined, is the basic concept of the stand valid in mixed species forests? The spatial variability of species mixtures changes with spatial scale and it would be necessary to determine the scale first.

This last consideration poses the distinction between mixed species stands and mixed species forests. We illustrate this with an example of a stand within a forest which is located on a larger landscape unit that serves as a matrix for such a forest. In this case if the mixture pattern is by groups it would be interesting to evaluate the mixing effect in the contact zones between species.

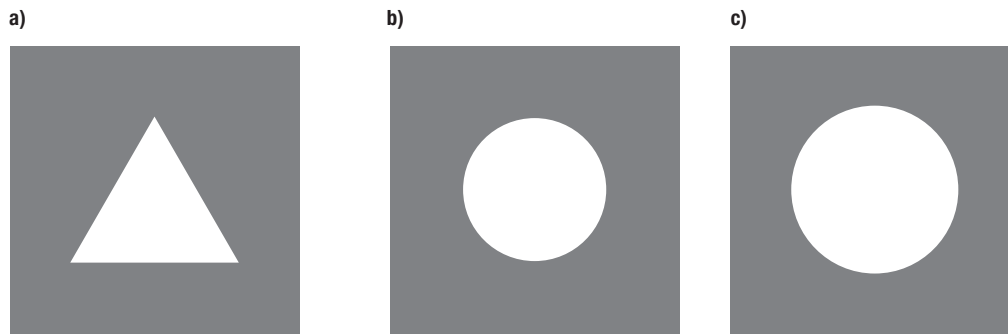


Figure 2. Effect of species pattern and scale on mixed Forest definition

In Fig. 2a and 2b each square represents a forest in which two species co-exist in an 80:20 proportion. Plot 2a has a larger contact zone between the species than 2b, so mixing effects are more likely to be significant in 2a. Fig. 2c has the same contact zone as in Fig. 2a but the proportion is approximately 60:40. The same analysis cannot be performed at the stand level as a stand within this forest could be defined as pure if the sample points lie inside a group of only one species. The conclusion is that both the spatial scale and the pattern of mixture need to be defined.

The same issue applies to the temporal definition of mixed forest. For example, would a mixture, measured as the proportion of the component species, be the same at some point in the future? How does a mixed forest evolve? Will the composition of the mixture and the species proportion be maintained with time? How might forest dynamics or management intervention affect the degree of mixture? Some of these questions have been partially answered in terms of developmental phases as mixed forests often occur in the late developmental phases of stands that originated as single-species (Larson, 1992) and that variation of species proportion over time can affect the dynamics of mixed forests (Puettmann *et al.*, 1992; Weiskittel *et al.*, 2009). The reverse statement in which dynamics affect species proportions is also possible. However, none of the definitions considered above dealt with spatial or temporal issues.

A consistent definition of mixed forest

It is therefore difficult to reconcile all points of view and to describe mixed forests in a single definition. Compositional and structural aspects are the easiest features

to use to describe a mixture of tree species in a forest, although it would be desirable to add spatial limits. Developmental definitions are problematic because in large forested areas it is plausible to have several stages occurring in close proximity. In addition, a detailed knowledge of the natural disturbance regime or management practices that have led to the current situation is required. The inclusion of functional aspects in a definition should not be based only on biodiversity-productivity relationships even if identification of competition or facilitative effects could alter management prescriptions, because other regulating aspects like nutrient dynamics are affected by species composition

Thus, a managerial definition should include all aspects discussed above plus the economic and social dimensions of forests, thus a reference and broad definition is preferred over a final or closed definition. We propose the following reference definition:

A mixed forest is a forest unit, excluding linear formations, where at least two tree species coexist at any developmental stage, sharing common resources (light, water, and/or soil nutrients). The presence of each of the component species is normally quantified as a proportion of the number of stems or of basal area, although volume, biomass or canopy cover as well as proportions by occupied stand area may be used for specific objectives. A variety of structures and patterns of mixtures can occur, and the interactions between the component species and their relative proportions may change over time.

This can be considered a high-level definition which encompasses all previous attempts to define mixed forests. We stress the need to explicitly modify or adjust this definition in any working situation in order to compare research or management results when classifying a mixed forest. Thus, it is necessary then to indicate the following criteria:

- the dimension of the forest unit assessed (stand, forest, landscape)
- the developmental stage (initiation phase, stem-exclusion, understorey reinitiation, old-growth)
- the occurrence and form of mixture (by individuals or by group)
- the temporal dimension of the study (static, dynamic) and
- the main driver of species richness-ecosystem functioning relationship to be assessed (facilitation, niche differentiation, competition).

Without explicitly defining these criteria the definition is worthless. This reference definition should be tested against existing forest classification systems (e.g. European Forest Types) or long term experimental networks in order to assess its capability to identify changes in key indicators of sustainability or the implications of changing management scenarios. We aim to examine these features in EuMIXFOR network.

Recent research perspectives where the definition might be tested

The study of mixed forests has led to a large body of literature in recent years indicating the range of benefits or ecosystem services obtained from mixed forests in Europe. They show the perspectives under which new research pathways can be developed. The following sections discuss some of the growth dynamics of mixtures, silvicultural considerations for converting pure stands to mixtures, and some economic considerations, while noting where some important knowledge gaps remain and where the definition might be tested.

Species interaction and species richness – ecosystem functioning

The interaction between two individuals, either of the same or different species, is usually assessed as an effect that can be positive, negative or neutral. Trees can interact in many ways but the negative (competitive) interactions have probably been the most widely studied in forests (Larocque *et al.* 2013). Due to their simplicity, the intraspecific interactions in monocultures are relatively easy to examine. However, in mixtures there is also inter-specific competition, which may (or may not) be weaker than the intra-specific

competition leading to a reduction in competition in the mixture (Vandermeer, 1989), due to niche partitioning. This is also sometimes referred to as the competitive production principle (Vandermeer, 1989). Niche partitioning can result when different species acquire resources in different ways (e.g. root stratification resulting in different water sources), which enables them use a greater proportion of available resources. Another important interaction that can occur in mixtures is facilitation. This occurs when one species has a positive effect on other species (Vandermeer, 1989). In practice it is difficult to differentiate between competitive reduction (niche differentiation, competitive production) and facilitation effects (Larocque *et al.*, 2013) and all of these are often collectively described as complementarity (Loreau & Hector, 2001). Disentangling the mechanisms that drive species interactions in mixed forests is a major challenge in both ecology and forestry.

Two approaches are typically used to analyze the interactions in mixed forests: analyzing the pattern of the interaction itself or analyzing the mechanisms driving the interaction. The study of inter- and intra-species interactions in mixed forest is often based on net effects (Forrester, 2014) because of the difficulty in separating the effects of the different mechanisms that influence the interspecific interactions (Callaway and Walker 1997).

Any of these complementary interactions can lead to *overyielding* where higher production in mixtures is expected compared to that of monocultures of the same size, or *transgressive overyielding* where a mixture produces more than the component species in pure stands (Pretzsch & Schütze, 2009). However, overyielding is not straightforward because it is usually constrained by the sampling effect hypothesis (Begon *et al.* 1996), which postulates that the more species that occur in a stand, the more likely it is that there will be a species that could be especially productive. Recent studies have shown complementary effects for a variety of mixtures with European beech (Dieler and Pretzsch, 2013; Metz *et al.*, 2013). Interactions can also show positive outcomes like mutualism (both species gain) and commensalism (one species gains and the other is unaffected). Gains and losses can be evaluated in terms of growth, survivorship, reproduction (Begon *et al.*, 2006) or fitness.

In reviewing species interactions in mixed forests Forrester (2014) argued that the interactions between a given pair of tree species can change along spatial or

temporal gradients in resource availability of climatic conditions. He also showed that complementarity increased as soil water (or nutrient) availability decreased when interactions reduced competition for water (or mixtures contained nitrogen fixing species). This is consistent with the stress-gradient hypothesis that suggests that facilitation increases and competition decreases with increasing abiotic/biotic stress (Bertness & Callaway, 1994).

Several spatial changes in species interactions suggested that the species interactions improved nutrient availability. For example, in mixtures of beech and oak overyielding was found on low fertility sites whereas no effect or a slight reduction in productivity appeared on fertile sites (Pretzsch *et al.* 2013). A similar effect was found by Río & Sterba (2009) for mixtures of Scots pine and Pyrenean oak. Temporal changes in species interactions have also been reported. For example, Pretzsch *et al.* (2013) found that drought stress could be reduced during harsh years in oak-beech stands and Río *et al.* (2014) measured the difference of basal area growth indices in mixed and pure stands. The results indicated strong competitive interaction in good growing seasons in oak-beech and spruce-beech mixtures whereas in years of poor growing conditions complementary effects were more important.

In contrast to these studies that show increasing complementarity with decreasing soil resource availability, complementary can also increase as growing conditions improve (Pretzsch *et al.*, 2010; Forrester *et al.*, 2013). This may result when the species interactions improve light absorption because as growing conditions improve, competition for light will probably increase and any interactions that improve light absorption or light-use efficiency will become more important (Forrester, 2014). Consistent with this pattern, complementarity increased with growing conditions in Silver fir and Norway spruce mixtures and this effect was associated with changes in canopy structure and crown architecture that improved light absorption on sites with more favourable conditions, but not on poorer sites (Forrester and Albrecht, 2014). There are relatively few studies that have examined the spatial or temporal dynamics of species interactions in mixtures. However, such knowledge is required for development of resource efficient and resilient production systems, future research should shift to why and where mixed species forests may out-yield neighbouring monocultures. Gradient studies are useful in such research tasks (Pretzsch *et al.* 2014), and studies

that also examine the processes driving the patterns will be particularly useful to understand these growth dynamics (Forrester, 2014).

Biomass partitioning between aboveground and belowground can vary with size, and temporal or spatial changes in resource availability (Poorter *et al.*, 2012; Schall *et al.*, 2012), and species interactions may alter all of these (Forrester, 2014). However, few studies have examined belowground productivity in mixtures and even fewer have compared above- and belowground productivity (Forrester *et al.*, 2006; Epron *et al.*, 2013). Belowground overyielding has not been demonstrated to occur in mature temperate forests (Meinen *et al.*, 2009a, 2009b; Jacob *et al.*, 2013) although root differentiation led to higher fine root productivity in young stands (Lei *et al.* 2012) whereas in boreal forests fine root overyielding was observed in mature stands originated after fire (Brassard *et al.*, 2011). Interspecific competition can also have a strong impact on crown structure (Bayer *et al.*, 2013) and crown allometry (Dieler & Pretzsch, 2013). In this regard the study of crown plasticity by terrestrial laser scanning is a promising tool (Seidel *et al.*, 2011; Metz *et al.*, 2013).

Stand density can also influence complementarity (Forrester, 2014), but effects are variable. As density increases, some studies find that complementarity increases (Boyden *et al.*, 2005; Amoroso & Turnblom, 2006; Condés *et al.*, 2013; Forrester *et al.*, 2013), while in others find that complementarity decreases (Boyden *et al.*, 2005; Río & Sterba, 2009; Condés *et al.*, 2013). Whether complementarity increases or decreases will probably depend on the main types of species interactions (light, water or nutrients, and competition or complementarity) and how the change in density influences these resources (Forrester, 2014). Changing stand density is a major silvicultural tool used for managing forests and these studies indicate that modifications of density could be a valuable tool for managing complementarity in mixtures. However, very few studies have quantified the processes behind these patterns and this information would be very useful for developing silvicultural regimes for mixtures.

Conversion of monocultures and stand density in mixed-species stands

Mixed forests also feature prominently in the debates over future trends in forestry. The continuous cover forestry approach recognizes the role of mixed

forests in enhancing structural diversity by diversification of monospecific plantations (Pommerening & Murphy, 2004)

Conversion of pure forest stands into mixed-species structures is becoming a common practice in Europe with the objective of both increasing the resistance and resilience of plantations or to convert gradually conifer plantations into broadleaved stands. The conversion of potentially unstable pure stands to more adapted mixed-species forests should be considered a priority in forest management (Spiecker, 2003; Ammer *et al.*, 2006; Knoke *et al.*, 2008). The success of converting a pure stand into a mixed-species one depends on both the species involved and the method of conversion. For example, De Schrijver *et al.* (2009) showed that the harvest method has an impact on the Ca and Mg nutrient cycling, when converting Scots pine plantations into a birch-pine stands on sandy soils. For the conversion of pure Norway spruce stands into mixed stands with European beech direct seeding or planting in advance have been proven to be successful measures (Ammer & Mosandl, 2007) followed by the strip cutting method to promote underplanted Douglas-fir and beech (Petritan *et al.*, 2011). In any case, long lasting and successful conversion of pure into mixed-species forests needs a better understanding of interactions between species and the influence of site factors (Mason & Connolly, 2014).

The process of conversion also influences other forest communities, like soil fauna that are enriched after conversion from pure to mixed stands (Ammer *et al.*, 2006; Chauvat *et al.*, 2011) and soil properties like available phosphorus content are favored in mixed forests after conversion (Slazak *et al.*, 2010). Soil treatment influences survival rates in Mediterranean conditions although sapling growth is not affected (Fonseca *et al.*, 2011)

Size-density relationship has been long studied in pure and mixed-species forests as it has a notable impact on forest yield. In forestry practice, Reineke's stand density index (SDI, Reineke, 1933), an analogous relationship to Yoda's 3/2 self-thinning boundary, has been used to manage density in even-aged single-species forests. The current SDI is compared to a species-specific maximum value (SDI_{max}) for determining the stand's relative density (RD) which is used to determine important stand development phases in even-aged forests.

A comparable index is lacking for mixed stands, although some attempts have been made. For example,

Sterba and Monserud (1993) modeled maximum density in uneven-aged mixed stands at discrete points of time as a function of dominant height. Refinement of this model leads to the estimation of maximum density for different admixtures (habitat type) and skewness of the diameter at breast height distribution. Dean and Baldwin (1996) introduced the idea that that maximum SDI is negatively correlated with specific gravity for conifers in single-species forests, so mechanistically a site can be occupied by a maximum density of a species based on the wood properties of the species. Woodall *et al.* (2005) extended the idea to mixed forests by using an average wood density for the mixture. More recently, Ducey & Knapp (2010) modified the approach to correspond more closely with the additive SDI for single-species uneven-aged stands developed by Long & Daniel (1990). However, Ducey and Knapp (2010) also presented arguments that accounting for mixed species density should have a nonlinear component. Other approaches include a generalization of Reineke's rule based on resource sharing and experimental calibration for mixed stands have been performed for beech, pedunculate oak and Norway spruce (Rivoire & Moguedec, 2012) whereas site factors and species composition have been identified as drivers of maximum density size-density relationship (Reyes-Hernández *et al.*, 2013).

Mixed forest stand density and structure can be assessed using airborne and terrestrial laser scanning as a management and research tool. The application of LiDAR technology to forest inventory has been proved effective in analyzing forest structure (stem and crown dimensions) in mixed forests (Ducey *et al.*, 2013). Another interesting technique is photogrammetry based on stereo images that can accurately predict volume and basal area at plot level (Straub *et al.*, 2013).

Valuation of ecosystem services

Most of the above topics relates to the provision service timber production. Timber production gives a financial return, and Knoke *et al.* (2008) argues that admixtures of species can reduce financial risk. Schou (2012) finds that a mix of two species is sufficient for such a gain and that more species only adds a marginal gain. However, one has to be aware of the unit of comparison for such studies. If two species are mixed (in equal shares) on a stand of two hectares, the portfolio is identical to one hectare of one species and one hec-

ture of the other species. Therefore, if the decision unit is higher than a single stand (which it typically will be), a potential gain from reduction of financial risk relies on increased silvicultural flexibility. If this is not present there is no financial risk reduction. Jacobsen & Thorsen (2003) shows that an option value may be present in mixed forests facing a risk of climate change; the reason being that if a forest manager can postpone the decision of the final tree species until he knows better how climate and thereby tree growth develops, then he may gain by postponing the decision. Again such an option value relies on the silvicultural feasibility of managing and potentially changing proportion of mixing species throughout a rotation. But commercial benefits could not explain alone the forest managers' decisions. Other values associated to mixed forests, such as environmental self-consumption of private landowners (incorporated into their decisions as, for example, the expected value of the land), environmental services to society in public forestry domains (with value, but without market price), the opportunities for tourism development, biodiversity conservation, etc. could affect the forest management.

Several studies have analyzed the preferences for mixed forests and the willingness to pay (WTP) for higher levels of tree diversity. For example, Nielsen *et al.* (2007) showed that users' WTP is higher in complex forest ecosystems with higher species composition and more diverse structure than in pure stands. Also Hanley *et al.* (1998) and Varela *et al.* (2013), among others, find a positive willingness to pay for a higher tree diversity. There are, however, also studies which report the opposite, for example Tyrväinen *et al.* (2003) found that pure stands were preferred over mixed stands. Some authors claim that preferences for forest type are highly dependent on cultural, regional and contextual factors (Edwards *et al.*, 2012).

The satiation of user's preferences regarding monocultures could lead to a higher preference of higher levels of tree species composition (Riera *et al.*, 2012). Biodiversity per se has a high welfare economic value and people have shown a high WTP for this (*e.g.* Campbell *et al.*, 2014; Jacobsen *et al.*, 2008), much higher than valuing diversity from common species (Bakhtiari *et al.*, 2014 compared to Campbell *et al.*, 2014). While mixed forests may have a higher Shannon index for example, it may be questioned whether it is better suited for conserving endangered species. In a meta-

study Paillet *et al.* (2010) find evidence of higher biodiversity in unmanaged forest than managed, but were not able to find differences between management. Eventhough Halme *et al.* (2010) question their findings, there is no doubt that the question of whether mixed forests have superiority over single species forests with regard to conserving endangered species, will have to be studied further. And for this purpose it may be useful with the definition and specification points suggested in this paper.

Conclusions

The increasing importance of mixed forests is a reflection of an increasing complexity of societal demands upon forest ecosystems, where mixed forests may be expected to have higher levels of resilience and resistance to environmental hazards, and a more diverse portfolio of environmental services. Forest managers and researchers should face this challenge with an appropriate understanding of the underlying mechanisms that control the interactions between species in order to more adequately predict the outcomes of forest operations'. EuMIXFOR is a timely research network supported by the COST framework in which the state of the art, gaps and future research directions regarding mixed forests will be addressed. The first critical step is the agreement on a consistent and reference definition of mixed forest that must be tested in order to make research and management results truly comparable. This work is the outcome of such agreement within EuMIXFOR network. Future perspectives of research on mixed forest have identified that case studies and retrospective analysis will continue to be an important source of experimental evidence of patterns and processes. Gradient studies, experimental design approaches, and model simulations regarding species interactions and responses to hazards, size-density relationships and its implication in silviculture, conversion of monocultures to mixed-species forest and economic valuation of ecosystem services provided by mixed forests are important topics in current research and they will foster future research.

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