

1 **Knowledge gaps about mixed forests: what do European forest** 2 **managers want to know and what answers can science provide?**

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60 **Abstract**

61 Research into mixed-forests has increased substantially in the last decades but the extent
62 to which the new knowledge generated meets practitioners' concerns is unknown. Here
63 we provide the current state of knowledge and future research directions with regards to
64 10 questions about mixed-forest functioning and management identified and selected by
65 a range of European forest managers during an extensive participatory process. The set
66 of 10 questions were the highest ranked questions from an online prioritization exercise
67 involving 168 managers from 22 different European countries. In general, the topics of
68 major concern for forest managers coincided with the ones that are at the heart of most
69 research projects. They covered important issues related to the management of mixed
70 forests and the role of mixtures for the stability of forests faced with environmental
71 changes and the provision of ecosystem services to society. Our analysis showed that
72 the current scientific knowledge about these questions was rather variable and
73 particularly low for those related to the management of mixed forests over time and the
74 associated costs. We also found that whereas most research projects have sought to
75 evaluate whether mixed forests are more stable or provide more goods and services than
76 monocultures, there is still little information on the underlying mechanisms and trade-
77 offs behind these effects. Similarly, we identified a lack of knowledge on the spatio-
78 temporal scales at which the effects of mixtures on the resistance and adaptability to
79 environmental changes are operating. Our analysis concluded with an identification of
80 future research challenges on mixed-forest management and functioning which may
81 help researchers to better design future research initiatives and to facilitate the transfer
82 of new knowledge into practical outcomes.

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

85 **1. Introduction**

86 In recent years, the study of mixed forests has been the focus of increasing research
87 efforts, in particular the consequences of admixing tree species for the productivity and
88 stability of forest systems. This has generated a substantial amount of new knowledge
89 (e.g. Pretzsch et al., 2013; Vilà et al., 2013; Morin et al., 2014; Tobner et al., 2016;
90 Liang et al., 2016; van der Plas et al., 2016; among others), and the consolidation of
91 important scientific initiatives and networks (Baeten et al., 2013; Bravo-Oviedo et al.,
92 2014; Verheyen et al., 2016). From the research perspective, the recent advances in the
93 understanding of mixed forests functioning are of unquestionable value, but the extent
94 to which this information is responding to practitioners' concerns remains unknown.

95 We addressed this issue via a collaborative work in the context of the EuMIXFOR
96 research network (Bravo-Oviedo et al., 2014) in which researchers from 30 different
97 European countries participated. The study was divided into three steps. First, we
98 conducted a Pan-European survey with the objective of identifying key questions
99 related to mixtures that, from the perspective of forest managers, still require further
100 research attention. Second, we ranked these questions by relevance according to the
101 views of an independent set of European practitioners obtained via an online
102 prioritization exercise. Finally, we evaluated current scientific knowledge for the
103 highest ranked questions and we identified future research challenges in relation to
104 them. The ultimate aim of our work was to reduce the commonly reported gap between
105 knowledge generated from research and that required by forest managers (see
106 Petrokofsky et al., 2010). In that respect, we expect our analysis will provide both (i)
107 information to the research community on the priority knowledge needs of forest
108 practitioners and (ii) information to the practitioners on the current state of knowledge
109 regarding the topics of their concern. Finally, we expect that the identification of

110 research challenges (based on the questions received from the practitioners) may help
111 researchers to contextualise and design future research initiatives and may also facilitate
112 the translation of new knowledge into practical outcomes.

113 **2. Collection and prioritization of research questions by forest managers**

114 2.1 Collection of questions

115 Each representative of the individual European countries that participated in the
116 *EUMIXFOR* network contacted forest managers from that country who had expertise in
117 the management of mixed-forests in either public or private ownership. We asked the
118 managers to provide a list of the 5 – 10 key questions about mixtures for which they
119 would like more information from the research community (preferably in the form of an
120 interrogative sentence). Fifty-three forest managers from 15 countries responded to this
121 request providing 289 questions (Fig. 1). The set of questions from each country was
122 added sequentially to the pool of questions, and the last sets of questions did not add
123 further information, suggesting that the main questions had been gathered. A
124 multidisciplinary group of six experienced forest researchers (LC, CC, ML, BM, QP
125 and KV) within the network classified each question into eleven broad themes (e.g.
126 timber production, species interactions...) during a one-day workshop. Questions within
127 each theme were then combined (when overlapping) and rephrased (if they were
128 unclearly formulated or related to a very specific type of mixture) by this group of
129 researchers. During this process, the only questions discarded were those that did not
130 relate to mixtures. The process concluded with the formulation of 30 questions covering
131 most of the replies originally received (Table S1).

132

133 2.2 Prioritization process

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



142

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

147 The BWS method (Finn and Louviere, 1992; Louviere et al., 2013) is a discrete choice
148 task in which each respondent is asked repeatedly to choose the most important and the
149 least important item from among randomly selected subsets of the original set of items,
150 in this case of 4 out of the 30 questions. BWS forces respondents to discriminate among
151 the presented alternatives, thus preventing some of the problems associated with other
152 ranking methodologies, such as anchoring bias, i.e. the tendency of respondents to
153 consistently use the middle points or one of the end points when using rating scales
154 (Flynn et al., 2007; Rudd and Lawton, 2013). The prioritization exercise was conducted
155 using an internet-based survey platform (SurveyGizmo, Boulder, CO, USA).

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

163 **3. Revision of the current state of knowledge in relation to forest managers'** 164 **questions**

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

172 3.1 Stability

173 ▪ *Which mixtures of species provide the best resistance and best resilience to climate*
174 *change and natural disturbances? (#1)*

175 ▪ *Are mixed forests more resistant and resilient to climate change and natural*
176 *disturbances? (#2)*

177 In recent years, the question of whether mixed forests are better able to cope with
178 environmental change than monocultures has been a focus of attention (see for example
179 the reviews by Thompson et al., 2009; Bauhus and Schmerbeck, 2010 or Scherer-
180 Lorenzen, 2014). The concepts of resilience and resistance have been addressed and
181 defined in many different ways (Brand, 2009). Here, we follow the approach of
182 Hodgson et al., (2015) and we consider resilience to encompass both resistance and
183 recovery; with the first being the capacity of the system to absorb an exogenous
184 disturbance and the second its capacity to come back to an equilibrium after being
185 disturbed (see also Oliver et al., 2015). Forest resilience can be approached at the level
186 of periodic stresses (e.g. drought episodes) or of disturbances (e.g. windstorms, fires)
187 (see Trumbore et al., 2015). In the case of most European forests, there is a large
188 consensus that the impacts of both types of stressor are expected to increase with
189 climate change (Seidl et al., 2011). The response of forests to periodic stresses relates to
190 the concept of ecosystem stability, a concept that has been largely investigated in
191 grassland ecosystems, where diversity helps to maintain the productivity of ecosystems
192 subject to climate variations (Tilman et al., 2006; Isbell et al., 2015). The diversity-
193 stability relationship in forest ecosystems is less clear (Thompson et al., 2009), although
194 some comprehensive studies such as the ones by Morin et al., (2014) and Jucker et al.,
195 (2014) also reported more stable productivity of mixed-forests over time. Such
196 stabilizing effects might be mediated by a reduction of the competition among species

197 for growing resources (i.e. functional complementarity (Loreau and Hector, 2001)),
198 asynchronous species-intrinsic responses to environmental fluctuations (Morin et al.,
199 2014) or by temporal shifts in species interactions (i.e. temporal complementarity) (del
200 Rio et al., 2017).

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

218 Similarly to biotic damages, the role of tree diversity in the capacity of forests to resist
219 severe abiotic disturbances (such as catastrophic windstorms or wildfires) is unclear and
220 appears to be more dependent on structure and species combinations than on diversity
221 (Dhôte, 2005; Grossiord et al., 2014; Pereira et al., 2014; Forrester et al., 2016). In

222 contrast, tree diversity is generally considered to enhance the capacity of forests to
223 recover from disturbances although this has been scarcely tested in field studies since it
224 requires long-term monitoring and adequate information about the state of the forest
225 prior to the disturbances. The higher resilience of mixtures to severe disturbances might
226 be mediated by the higher diversity and higher redundancy of traits relevant to tree
227 response to environmental changes (e.g. resprouting capacity, seed bank longevity) that
228 these stands may present (Yachi and Loreau, 1999; Laliberté et al., 2010; Puettmann,
229 2011; Sánchez-Pinillos et al., 2016).

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

239 3.2 Provision of ecosystem services

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

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

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

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

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

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

269 Positive DPRs are related to selection (when changes in the relative yields of species in
270 a mixture are non-randomly related to their yields in monoculture; Loreau and Hector,

271 (2001)) and complementarity resulting from (i) competitive reduction (when
272 competition is reduced in mixtures compared to pure stands) or (ii) facilitation (when a
273 species improves the functioning of another species) (Vandermeer, 1989).
274 Complementarity arises from inter-specific differences in physiology, phenology or
275 morphology or from intra-specific differences that result from inter-specific
276 interactions, and is affected by stand structure (Richards et al., 2010; Forrester and
277 Bauhus, 2016). There is important variability among DPRs, even for a given species
278 pool. The Monteith primary production model may be used as a framework to explain
279 how the slope of the DPR changes along spatial or temporal gradients in resource
280 availability or climatic conditions (Forrester and Bauhus, 2016). Complementarity is
281 predicted to increase as the availability of a given resource declines (or as climatic
282 conditions become harsher) if interactions among associated species result in an
283 improvement of the availability, uptake or use-efficiency of that resource (or if
284 interactions improve the climatic condition). Functional differences among admixed
285 species appear to be a key condition for overyielding to occur (Zhang et al., 2012), but
286 the net effect of these functional differences on overyielding depends on how they can
287 reduce climate constraints / increase availability of limiting resources on a particular
288 site.

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

290 *Carbon sequestration*

291 The effects of tree species diversity on C sequestration may be assessed by considering
292 (i) the biologically-mediated processes that drive the rates of C gain and loss and the
293 size and longevity of C stocks, and (ii) the processes that determine the associated social
294 and economic values (Diaz et al., 2009a; Diaz et al. 2009b). While the contribution of
295 tree diversity to the net C uptake in aboveground tree components may be derived from

296 DPRs, its impacts on belowground C storage, including roots and soils, remain much
297 less documented (Hulvey et al., 2013). Because trade-offs at the individual tree species
298 level prevent the maximizing of C sequestration across multiple C pools (e.g. root vs
299 shoot biomass; Hulvey et al., 2013), maximizing forest C sequestration is expected to be
300 achieved by using selected combinations of species traits. The complex effects of tree
301 species diversity and identity on C storage are well illustrated when analysing soil C
302 stocks. Dawud et al., (2016) observed a limited influence of tree species diversity and
303 identity on the overall C soil storage (0-40 cm), but contrasting effects on the
304 distribution of C within the soil profile. Diversity tended to increase C in deeper layers;
305 by contrast, the effect of diversity on the forest floor C stock was inconsistent, in
306 agreement with Handa et al. (2014) who clearly showed that the functional diversity of
307 both decomposers and leaf litter, not simply litter species richness, promotes C and N
308 cycling. As opposed to diversity, species identity tended to influence C storage in the
309 upper forest floor layers. If confirmed by other studies, tree species diversity would
310 therefore mainly benefit the longevity of C stocks through its effects on C storage in the
311 deeper soil layers.

312 *Plant and animal diversity*

313 Canopy trees represent only a small part of forest biodiversity. The impacts of tree
314 diversity on plant, animal and fungal diversity are complex. On one hand, mixed forests
315 can be more productive, they also present higher structural heterogeneity which may
316 provide more diverse above- and belowground microhabitats than monocultures, and
317 may therefore host a greater number of organisms (De Deyn et al. 2004). On the other
318 hand, neutral or negative effects of tree diversity may be observed in mixed forest
319 where a dilution of each individual tree species may eliminate organisms that are
320 dependent on particular tree species (Ampoorter et al., 2014; Tedersoo et al., 2016). In a

321 literature review, Cavard et al., (2011) examined existing empirical evidence that tree
322 mixtures promote the diversity of understory plants, songbird, soil fauna, and
323 ectomycorrhiza in northern forests. They found no evidence of the existence of
324 organisms uniquely associated with mixtures, species richness simply reflecting, at best,
325 the accumulation of organisms associated with each canopy tree species. They also
326 reported that tree diversity improves the diversity of understory plants (but see Barbier
327 et al., 2008), avian and ectomycorrhizal communities (see also Bibby et al., 1989).
328 Although many studies found positive effects of mixtures on earthworm or
329 microarthropod diversity (see Korboulewsky et al., 2016), no general trend emerged on
330 the relationship between mixed forests and soil fauna diversity.

331 *Provision of multiple ecosystem services*

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

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

343 The degree of multifunctionality of a forest can be determined by the number of
344 ecosystem functions exceeding a predefined threshold value (Byrnes et al., 2014). Using
345 such an approach, van der Plas et al., (2016) showed that multifunctionality increased

346 with species richness for moderate levels of functioning, while it decreased when high
347 function levels are desired. One may therefore conclude that the simultaneous
348 maximisation of all functions at a stand level is not achievable as a result of trade-off
349 between functions.

350 ▪ *Which mixture of species (or functional groups) should be used to optimize*
351 *specific or combined management targets (e.g. productivity, biodiversity,*
352 *stability...)? (#4)*

353 ▪ *Which positive and negative effects on different ecosystem functions (e.g.*
354 *productivity, litter decomposition, stem quality) can occur when mixing*
355 *particular species? (#6)*

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

370 models, such as those developed for growth (Forrester and Tang, 2016), appear quite
371 promising as they combine the most relevant mechanisms and their interactions.

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

379 For some functions, however, the relationship with tree species diversity remains much
380 less documented or general patterns have not been discerned (Nadrowski et al., 2010).
381 This is the case, among others, for those functions and processes that are more strongly
382 affected by site conditions such as belowground processes and biogeochemical cycling
383 (Scherer-Lorenzen, 2014). In addition to the identity effects discussed above, the
384 possible context dependency of the Diversity Ecosystem functions Relationships
385 (DERs) could also explain the lack of net diversity effects when encompassing a range
386 of sites, contrasting DERs slopes between sites being driven by environmental factors.

387 3.3 Management

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

390 The silvicultural treatments applied to any mixture should reflect the management
391 objectives chosen for the forest while respecting edaphic factors and species
392 composition and characteristics. A useful framework for evaluating the potential
393 effectiveness of silvicultural interventions at different phases of stand development is

394 provided by a model of stand dynamics (Oliver and Larson, 1996) which separates
395 stand development into four stages: stand initiation, stem exclusion, understorey
396 reinitiation and old-growth (note that the last stage is rare in many managed forests).
397 The creation of mixtures is best achieved in the first and third stages, whereas in the
398 second stage thinning is used to ensure the survival of an existing mixture. However, at
399 all stages, careful tending can be essential to ensure that the balance of a desired mixture
400 is maintained.

401 During the stand initiation stage, acceptance of natural regeneration of a range of
402 species that are suited to the site is often the best and most cost-effective way of
403 developing a mixed stand. This approach can be combined with planting so that the
404 regeneration forms the matrix between planted groups of a desired species (Saha et al.,
405 2013), or can be favoured to create a two storied stand (Frivold and Groven, 1996;
406 Stanturf et al., 2014). Two-storied mixed stands can also be created by deliberately
407 underplanting fast growing pioneer tree species with slower growing and shade tolerant
408 broadleaves or conifers (Pommerening and Murphy, 2004; Kelty, 2006; Paquette and
409 Messier, 2013). Planting of mixtures is an option on nutrient poor soils where a more
410 nutrient demanding species is mixed with one adapted to such sites, as is the case for the
411 pine/spruce mixtures reported from the British Isles (Gabriel et al., 2005; Mason and
412 Connolly, 2014) and Poland (Bielak et al., 2014) or where a nitrogen fixing species is
413 mixed with another valuable timber species such as walnut (*Juglans regia* L.) or
414 *Eucalyptus* spp. (Clark et al., 2008; Forrester et al., 2011).

415 Once the trees have closed canopy (stem exclusion), a period of intense inter-tree
416 competition begins which can be mediated by the selective removal of individual trees
417 or species (a.k.a 'thinning'). Where species are of compatible growth rates and shade
418 tolerance, there is little need to adjust thinning strategies from practice in pure stands.

419 The challenge occurs where the competition from one species can disadvantage the
420 growth of a favoured species, as occurs with aspen (*Populus tremuloides* Michx.) and
421 white spruce (*Picea glauca* (Moench) Voss) in boreal mixedwoods (Filipescu and
422 Comeau, 2007). In such instances, thinning will need to favour stems of a more
423 vulnerable but desirable species by removing immediate competitors. Other examples
424 include mixtures of oak and more shade tolerant tree species (such as beech) where
425 thinning is mandatory to prevent the latter outcompeting the more valuable oak (Hein
426 and Dhôte, 2006; Johnson et al., 2009).

427 As the trees age, the canopy either begins to open up naturally or small gaps are created
428 through thinning. As a result, the increased light on the forest floor allows tree seedlings
429 of a range of species to become established ('understorey reinitiation'). With control of
430 ungulate browsing and careful tending, over time such seedlings (planted or naturally
431 regenerated) can be promoted into the upper canopy layers and can be used to help
432 convert a regular structure to an irregular one (Mosandl and Kleinert, 1998; Nyland,
433 2003; O'Hara, 2014). This process can be used as a means of converting pure planted
434 stands to mixed irregular forests, as in the conversion of Norway spruce to mixed
435 conifer-broadleaved stands in some regions of central and western Europe (Spiecker et
436 al., 2004; Ammer et al., 2008) or in restoring natural forest types after larch
437 afforestation in northern China (Mason and Zhu, 2014). The development and formation
438 of these mixed stands can be fostered by a range of irregular silvicultural systems
439 (Matthews, 1991) involving combinations of tree species of different functional traits.
440 While the general principles of the transformation process outlined above are well
441 understood, their formulation into silvicultural guidelines for the management of
442 particular species combinations in specific site conditions is often lacking. In part, this
443 major knowledge gap reflects the historic emphasis given to experimentation with

444 single species stands which means that the complexities of successfully manipulating
445 species mixtures over time are poorly described and little known.

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

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

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

464 For forest managers, any evaluation of benefits and costs from mixtures is heavily
465 dependent on financial returns from wood production rather than involving
466 consideration of wider aspects such as the relative delivery of ecosystems services
467 (Quine et al., 2013). Establishment costs can heavily influence the potential
468 profitability of mixtures. Saha et al. (2013), for example, showed that group plantings of

469 oak in broadleaved regeneration were cheaper to establish and maintain than
470 conventional pure oak planting in an analysis carried out in young (10-26 years old)
471 forest stands of central and southern Germany. Comparisons of the relative returns from
472 pure and mixed stands depend upon the anticipated yields from the two types of stands,
473 and a situation where a high yielding species is mixed with a less productive one often
474 results in lower total yield and a reduction in theoretical profits (Knoke et al., 2008).
475 However, if the probability of risks from disturbances (biotic or abiotic), which are
476 generally higher for pure stands, are calculated it can be shown that the mixed stand has
477 a higher outturn, especially for a risk averse investor/owner and where longer rotations
478 are incurred (Roessiger et al., 2013). In addition, a yield stimulus of 10%, depending on
479 product and rotation length, can offset any increased costs associated with planting and
480 managing mixed-species stands (Nichols et al., 2006). For example, if proper
481 allowance is made for any positive yield improvement from growing species in mixture,
482 then the financial performance of the mixture is better than that of the pure stand, as in
483 two-storied mixtures of birch (*Betula pendula* Roth. and *Betula pubescens* Ehrh.) and
484 Norway spruce (*Picea abies* (L.) Karsten) in Scandinavia (Valkonen and Valsta, 2001).
485 However, such results can be influenced by stand structure since the financial outturn
486 from single storied mixed stands of the same species was lower in the mixture than in
487 the pure stand (Fahlvik et al., 2011). These results highlight how evaluation of the
488 relative balance of the financial return from mixtures can be context dependent,
489 influenced by factors such as forest type and owner objectives (Felton et al., 2016).

490

491 **4. General discussion and future research directions**

492 We summarise above the current state of knowledge in relation to the ten highest ranked
493 questions related to mixed-forest management and functioning that are of major concern

494 from the view of European forest managers. Our exercise could be conceived as a
495 discussion between research suppliers and users: we consider that it has delivered
496 results of high interest for both groups. The questions for which forest managers
497 showed the most concern related to the capacity of mixed forests to respond to the
498 effects of climate change and/or to the occurrence of natural disturbances. This could be
499 explained by the recognized uncertainty of, and unpredictability associated with, these
500 events and to the fact that they are not “controllable” by the implementation of any
501 management strategy or action. Interestingly, these topics have been at the centre of
502 many research initiatives (see Table 1). There is a general agreement in the scientific
503 literature that mixtures are more resilient to natural disturbances than monocultures and
504 that they present more options for adaptation to climate change. However, some of these
505 positive aspects seem to be more related to the specific composition of the mixture than
506 to tree diversity *per se*, and additional efforts should be undertaken to assess which
507 combination of species or functional groups needs to be promoted to tackle potential
508 negative effects of predicted (or unexpected) environmental changes. Indeed, we share
509 the view of Jactel et al. (2016) that further research efforts in this topic might be
510 devoted to the understanding of potential trade-offs between species and communities
511 with regards to the resistance and recovery to different disturbances and environmental
512 changes. Improving our understanding of the spatio-temporal scales at which the effects
513 of mixtures on the resistance and adaptability to change are operating might also be
514 considered in future research projects (Table 1).

515 In contrast to the analysis of the underlying mechanisms behind the diversity – stability
516 relationship, which has received substantial attention from the research community, we
517 have poor information on how to manage tree mixtures over time and the cost (and
518 benefits) behind these systems. Accordingly, we were able to provide very few

519 evidence-based responses to the questions raised by the managers in relation to this
520 area. Once the scarce published literature on this topic was reviewed, we observed that
521 there is a critical lack of long-term research plots that explore and illustrate the
522 silviculture of mixed forests in different forest types (Table 1). Such plots are necessary
523 to validate the results of more theoretical studies as well as to support practice and the
524 development of guidelines for the management of mixed forests. For example, there are
525 many examples where high browsing pressure from ungulates prevents the
526 establishment of new mixed-species plantations (e.g. Bergquist et al., 2009) but very
527 little information on how to achieve protection from such browsing without high costs.
528 We also recognized there are almost no documented case studies which provide
529 operational evidence of the greater management flexibility presumed to be provided by
530 mixed forests, and very few integrated economic analysis showing the effects of a
531 greater use of mixtures on the provision of ecosystem services within the forestry-wood
532 chain. Such analyses may need to take proper account of uncertainty and risk and to
533 provide costs and revenues which are relevant to managers' needs (Table 1).

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

541

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.

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)	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); von Lüpke and Spellmann, (1999)	Establishment and analysis of long-term research plots; browsing problems during the first growing stages
#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)	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;

* 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 (+)

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

560 In conclusion, the results of our analysis show a general agreement between forest
561 managers' concerns and the topics that are at the heart of most research projects dealing
562 with mixed-forests. However, we have detected substantial differences in the amount of
563 available knowledge relating to the various questions provided by the managers.
564 Whereas most research projects have sought to evaluate whether mixed forests provide
565 more goods and services than monocultures and are more stable when faced with
566 environmental change (i.e. the *effects* of mixing, questions #2, #5), there is still little
567 information about the underlying mechanisms and trade-offs behind these effects

568 (although these questions are currently at the heart of a number of research initiatives
569 (Verheyen et al., 2016)). Finally, our results stress the critical need of generating
570 additional knowledge to provide forest managers with evidence-based silvicultural
571 guidelines allowing the establishment and maintenance of mixtures over time under
572 different environmental conditions.

573

574

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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 complex mixed stands?	51,51
#16	Do intimate mixtures provide more (or different) benefits compared to	50,57

	patch or landscape scale mixtures?	
#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
