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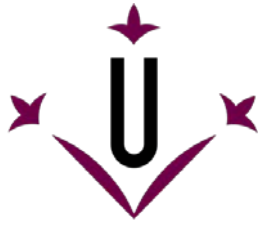
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Knowledge gaps about mixed forests: what do European forest managers want to know and what answers can science provide?

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

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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 highest
103 ranked questions and we identified future research challenges in relation to them. The
104 ultimate aim of our work was to reduce the commonly reported gap between knowledge
105 generated from research and that required by forest managers (see Petrokofsky et al.,

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106 2010). In that respect, we expect our analysis will provide both (i) information to the
107 research community on the priority knowledge needs of forest practitioners and (ii) brief
108 reviews of the current state of knowledge regarding the topics of their concern. Finally,
109 we expect that the identification of research challenges (based on the questions received
110 from the practitioners) may help researchers to contextualise and design future research
111 initiatives and may also facilitate the translation of new knowledge into practical
112 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. The sets of questions brought by the last
123 countries added to the list did not bring further information, suggesting that the main
124 questions had already been gathered and that adding new countries would not increase
125 the number of questions to be retained.

126 A multidisciplinary group of six experienced forest researchers (LC, CC, ML, BM, QP
127 and KV) within the network classified each question into eleven broad themes (e.g.
128 timber production, species interactions...) during a one-day workshop. Questions within

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129 each theme were then combined (when overlapping) and rephrased (if they were
130 unclearly formulated or related to a very specific type of mixture) by this group of
131 researchers. During this process, the only questions discarded were those that did not
132 relate to mixtures. The process concluded with the formulation of 30 questions covering
133 most of the replies originally received (Table S1).

134 2.2 Prioritization process

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

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STEP 1: COLLECTION OF QUESTIONS

53 managers from **15 countries** were asked to provide a list of the 5-10 key questions about mixtures



289 questions

STEP 2: CLASSIFICATION

A research multidisciplinary team classified, merged and rephrased the questions

30 questions

STEP 3: PRIORITIZATION

168 managers from **22 countries** participated to a questionnaire to identify the most important research questions

10 questions



143

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

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

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

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

164 **3. Revision of the current state of knowledge in relation to forest managers'** 165 **questions**

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

173 3.1 Stability

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

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178 In recent years, the question of whether mixed forests are better able to cope with
179 environmental change than monocultures has been a focus of attention (see for example
180 the reviews by Thompson et al., 2009; Bauhus and Schmerbeck, 2010 or Scherer-
181 Lorenzen, 2014). The concepts of resilience and resistance have been addressed and
182 defined in many different ways (Brand, 2009). Here, we follow the approach of
183 Hodgson et al., (2015) and we consider resilience to encompass both resistance and
184 recovery; with the first being the capacity of the system to absorb an exogenous
185 disturbance and the second its capacity to come back to an equilibrium after being
186 disturbed (see also Oliver et al., 2015). Forest resilience can be approached at the level
187 of periodic stresses (e.g. drought episodes) or of disturbances (e.g. windstorms, fires)
188 (see Trumbore et al., 2015). In the case of most European forests, there is a large
189 consensus that the impacts of both types of stressor are expected to increase with
190 climate change (Seidl et al., 2011). The response of forests to periodic stresses relates to
191 the concept of ecosystem stability, a concept that has been largely investigated in
192 grassland ecosystems, where diversity helps to maintain the productivity of ecosystems
193 subject to climate variations (Tilman et al., 2006; Isbell et al., 2015). The diversity-
194 stability relationship in forest ecosystems is less clear (Thompson et al., 2009), although
195 some comprehensive studies such as the ones by Morin et al., (2014) and Jucker et al.,
196 (2014) also reported more stable productivity of mixed-forests over time. Such
197 stabilizing effects might be mediated by a reduction of the competition among species
198 for growing resources (i.e. functional complementarity (Loreau and Hector, 2001)),
199 asynchronic species-intrinsic responses to environmental fluctuations (Morin et al.,
200 2014) or by temporal shifts in species interactions (i.e. temporal complementarity) (del
201 Rio et al., 2017).

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

219 Similarly to biotic damages, the role of tree diversity in the capacity of forests to resist
220 severe abiotic disturbances (such as catastrophic windstorms or wildfires) is unclear and
221 appears to be more dependent on structure and species combinations than on diversity
222 (Dhôte, 2005; Grossiord et al., 2014; Pereira et al., 2014; Forrester et al., 2016, Metz et
223 al, 2016). In contrast, tree diversity is generally considered to enhance the capacity of
224 forests to recover from disturbances although this has been scarcely tested in field
225 studies since it requires long-term monitoring and adequate information about the state

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226 of the forest prior to the disturbances. The higher resilience of mixtures to severe
227 disturbances might be mediated by the higher diversity and higher redundancy of traits
228 relevant to tree response to environmental changes (e.g. resprouting capacity, seed bank
229 longevity) that these stands may present (Yachi and Loreau, 1999; Laliberté et al., 2010;
230 Puettmann, 2011; Sánchez-Pinillos et al., 2016).

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

240 3.2 Provision of ecosystem services

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

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

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

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

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

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

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

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

291 *Carbon sequestration*

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

313 *Plant and animal diversity*

314 Canopy trees represent only a small part of forest biodiversity. The impacts of tree
315 diversity on plant, animal and fungal diversity are complex. On one hand, mixed forests

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

332 *Provision of multiple ecosystem services*

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

337 Multifunctional forest management requires that multiple ecosystem functions and
338 services are simultaneously sustained. Several studies, mainly from grassland

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339 experiments, demonstrated that the level of biodiversity needed to maintain multiple
340 functions was greater than the levels needed to maximize each individual function
341 (Hector and Bagchi, 2007; Lefcheck et al., 2015); considering multiple locations and
342 long time series in a changing environment further increases the needed level of
343 biodiversity to provide multiple functions (Isbell et al., 2011).

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

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

357 Although many ecosystem functions are on average positively associated with canopy
358 tree diversity (Nadrowski et al., 2010), there is often a considerable scattering around
359 the mean, and for a given diversity level, the outcome of the interactions may be either
360 positive, neutral or even negative, depending on the identities of the associated species
361 (Scherer-Lorenzen, 2014). Moreover, even when similar species are combined, the

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362 outcome still depends on the set of current environmental conditions, including resource
363 availability and climate constraints, as reported above for DPRs. From the manager's
364 perspective, this means that effective tree species selection has to consider not only the
365 functional differences between the investigated species for those traits involved in the
366 function of interest, but also how functional diversity is expected to translate into
367 positive effects given the environmental conditions at hand. While approaches using
368 functional diversity metrics (Laliberté and Legendre, 2010; Mouchet et al., 2010) and
369 empirical frameworks relating complementarity to resource availability and climate
370 (Forrester and Bauhus, 2016) may assist optimal species selection, process-based
371 models, such as those developed for growth (Forrester and Tang, 2016), appear quite
372 promising as they combine the most relevant mechanisms and their interactions.

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

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

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

388 3.3 Management

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

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

402 During the stand initiation stage, acceptance of natural regeneration of a range of
403 species that are suited to the site is often the best and most cost-effective way of
404 developing a mixed stand. This approach can be combined with planting so that the
405 regeneration forms the matrix between planted groups of a desired species (Saha et al.,
406 2013), or can be favoured to create a two storied stand (Frivold and Groven, 1996;
407 Stanturf et al., 2014). Two-storied mixed stands can also be created by deliberately
408 underplanting fast growing pioneer tree species with slower growing and shade tolerant

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409 broadleaves or conifers (Pommerening and Murphy, 2004; Kelty, 2006; Paquette and
410 Messier, 2013). Planting of mixtures is an option on nutrient poor soils where a more
411 nutrient demanding species is mixed with one adapted to such sites, as is the case for the
412 pine/spruce mixtures reported from the British Isles (Gabriel et al., 2005; Mason and
413 Connolly, 2014) and Poland (Bielak et al., 2014) or where a nitrogen fixing species is
414 mixed with another valuable timber species such as walnut (*Juglans regia* L.) or
415 *Eucalyptus* spp. (Clark et al., 2008; Forrester et al., 2011; Radosevich et al., 2016).

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

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

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

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

450 Conceptually, the presence of more than one species in a maturing stand should give
451 forest managers greater flexibility to adapt to changing objectives and to harvest
452 different products at different stages of a stand's development (Nichols et al., 2006).
453 However, it is difficult to find cases where this theoretical benefit has actually been
454 realised or where there has been a comparison with pure stands. One example occurred
455 in the UK in the 1960s when policy for public forests changed from developing a
456 strategic supply of timber for the market to maximising the return on investment. As a

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457 result, a silvicultural regime for management of nursing mixtures of conifers and
458 broadleaves in lowland Britain (Kerr et al., 1992) was changed from gradually removing
459 the conifers to favour the broadleaves to one of eliminating the broadleaves to favour
460 the faster growing conifers. The occurrence of aspen and white spruce in either two or
461 single storey mixtures in boreal Canada is another example where the combination can
462 allow managers to harvest either species for different products depending on market
463 conditions and demand (Comeau et al., 2005).

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

466 For forest managers, any evaluation of benefits and costs from mixtures is heavily
467 dependent on financial returns from wood production rather than involving
468 consideration of wider aspects such as the relative delivery of ecosystems services
469 (Quine et al., 2013). Establishment costs can heavily influence the potential
470 profitability of mixtures. Saha et al. (2013), for example, showed that group plantings of
471 oak in broadleaved regeneration were cheaper to establish and maintain than
472 conventional pure oak planting in an analysis carried out in young (10-26 years old)
473 forest stands of central and southern Germany. Comparisons of the relative returns from
474 pure and mixed stands depend upon the anticipated yields from the two types of stands,
475 and a situation where a high yielding species is mixed with a less productive one often
476 results in lower total yield and a reduction in theoretical profits (Knoke et al., 2008).
477 However, if the probability of risks from disturbances (biotic or abiotic), which are
478 generally higher for pure stands, are calculated (e.g. Neuner et al., 2015) it can be
479 shown that the mixed stand has a higher outturn, especially for a risk averse
480 investor/owner and where longer rotations are incurred (Roessiger et al., 2013). In

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481 addition, a yield stimulus of 10%, depending on product and rotation length, can offset
482 any increased costs associated with planting and managing mixed-species stands
483 (Nichols et al., 2006). For example, if proper allowance is made for any positive yield
484 improvement from growing species in mixture, then the financial performance of the
485 mixture is better than that of the pure stand, as in two-storied mixtures of birch (*Betula*
486 *pendula* Roth. and *Betula pubescens* Ehrh.) and Norway spruce (*Picea abies* (L.)
487 Karsten) in Scandinavia (Valkonen and Valsta, 2001). However, such results can be
488 influenced by stand structure since the financial outturn from single storied mixed
489 stands of the same species was lower in the mixture than in the pure stand (Fahlvik et
490 al., 2011). These results highlight how evaluation of the relative balance of the financial
491 return from mixtures can be context dependent, influenced by factors such as forest type
492 and owner objectives (Felton et al., 2016).

493

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

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

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

518 In contrast to the analysis of the underlying mechanisms behind the diversity – stability
519 relationship, which has received substantial attention from the research community, we
520 have poor information on how to manage tree mixtures over time and the cost (and
521 benefits) behind these systems. Accordingly, we were able to provide very few
522 evidence-based responses to the questions raised by the managers in relation to this
523 area. Once the scarce published literature on this topic was reviewed, we observed that
524 there is a critical lack of long-term research plots that explore and illustrate the
525 silviculture of mixed forests in different forest types (Table 1). Such plots are necessary
526 to validate the results of more theoretical studies as well as to support practice and the
527 development of guidelines for the management of mixed forests. We also recognized

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528 there are almost no documented case studies which provide operational evidence of the
529 greater management flexibility presumed to be provided by mixed forests, and very few
530 integrated economic analysis showing the effects of a greater use of mixtures on the
531 provision of ecosystem services within the forestry-wood chain. Such analyses may
532 need to take proper account of uncertainty and risk and to provide costs and revenues
533 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 Bauhus, 2016).

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

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545
546

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

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

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

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

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571 information about the underlying mechanisms and trade-offs behind these effects
572 (although these questions are currently at the heart of a number of research initiatives
573 (Verheyen et al., 2016)). Finally, our results stress the critical need of generating
574 additional knowledge to provide forest managers with evidence-based silvicultural
575 guidelines allowing the establishment and maintenance of mixtures over time under
576 different environmental conditions.

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998 **Supplementary information**

999

1000 **Table S1.** List of 30 questions ordered by their rank value (expressed on a 0–100 scale)
1001 after the prioritization exercise

1002

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

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