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► To cite this version:

Eckehard G. Brockerhoff, Luc Barbaro, Bastien Castagneyrol, David I. Forrester, Barry Gardiner, et al.. Forest biodiversity, ecosystem functioning and the provision of ecosystem services. *Biodiversity and Conservation*, 2017, 26 (13), pp.3005-3035. 10.1007/s10531-017-1453-2. hal-02625784

HAL Id: hal-02625784

<https://hal.inrae.fr/hal-02625784v1>

Submitted on 21 Jan 2025

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Forest biodiversity, ecosystem functioning and the provision of ecosystem services

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1 **Abstract**

2 Forests are critical habitats for biodiversity and they are also essential for the provision of a wide range
3 of ecosystem services that are important to human well-being. There is increasing evidence that
4 biodiversity contributes to forest ecosystem functioning and the provision of ecosystem services. Here
5 we provide a review of forest ecosystem services including biomass production, habitat provisioning
6 services, pollination, seed dispersal, resistance to wind storms, fire regulation and mitigation, pest
7 regulation of native and invading insects, carbon sequestration, and cultural ecosystem services in
8 relation to forest type, structure and diversity. We also consider relationships between forest
9 biodiversity and multifunctionality, and trade-offs among ecosystem services. We compare the concepts
10 of ecosystem processes, functions and services to clarify their definitions. Our review of published
11 studies indicates a lack of empirical studies that establish quantitative and causal relationships between
12 forest biodiversity and many important ecosystem services. The literature is highly skewed; studies on
13 provisioning of nutrition and energy, and on cultural services delivered by mixed-species forests are
14 under-represented. Planted forests offer ample opportunity for optimising their composition and
15 diversity because replanting after harvesting is a recurring process. Planting mixed-species forests
16 should be given more consideration as they are likely to provide a wider range of ecosystem services
17 within the forest and for adjacent land uses. This review also serves as the introduction to this special
18 issue of *Biodiversity and Conservation* on various aspects of forest biodiversity and ecosystem services.

19

20 **Key words:** Ecological processes, mixed-species forest, planted forest, tree diversity.

21

22

23

24 **Introduction**

25

26 Forests and woodlands harbour immense terrestrial and aquatic biodiversity and, especially in moist
27 tropical regions, represent the most species-rich habitat type worldwide (Mace et al. 2005; Lindenmayer
28 2009; Gibson et al. 2011). Pressures from human activities leading to forest loss, fragmentation and
29 degradation (FAO 2015) have already caused much biodiversity decline and homogenization
30 (Lindenmayer and Franklin 2002; Newbold et al. 2015; van der Plas et al. 2016b). These declines are
31 expected to continue (e.g., Newbold et al. 2015), especially in the rich forests of Central and South
32 America, South and Southeast Asia and Africa, although the rate of forest loss has been slowing in
33 recent years (Keenan et al. 2015). Conversely, the area of planted forests (including plantation forests) is
34 increasing and is currently ca. 7% of total forest cover (Payn et al. 2015).

35

36 Collectively, these trends in forest cover and condition are a major concern, not only because of the
37 implications for the conservation of biodiversity, but also because forests provide a wide range of
38 critically important ecosystem services such as climate regulation, biomass production, water supply
39 and purification, pollination, and the provision of habitats for forest species (Bauhus et al. 2010;
40 Thompson et al. 2011; Brockerhoff et al. 2013; Decocq et al. 2016; Liang et al. 2016; Mori et al. 2017).
41 There is also increasing evidence that the provision of ecosystem services is related to aspects of
42 biodiversity; there is a positive relationship between biodiversity and most ecosystem services (e.g.,
43 Hooper et al. 2005; Balvanera et al. 2006; Isbell et al. 2011; Gamfeldt et al. 2013).

44
45 A wide range of mechanisms have been proposed to explain the relationships between biodiversity and
46 ecosystem services. Niche complementarity in time and space, and complementarity of functional effect
47 traits and functional response traits are all likely to be involved (Isbell et al. 2011). Facilitation between
48 plant species growing together has often been found to lead to enhanced growth of certain tree
49 mixtures (Thompson et al. 2014). For example, at nitrogen-limited sites, tree species that are nitrogen-
50 fixers may enhance the growth of other tree species in mixed stands (e.g., Binkley 2003; Forrester and
51 Bauhus 2016). Resistance to disturbance is facilitated by forest and tree diversity, leading to a reduction
52 or dilution of resources (e.g., for herbivores), diversion or disruption, and multi-trophic interactions
53 (e.g., enhanced abundance and action of natural enemies) (Jactel et al. 2017). Finally, the so-called
54 'sampling effect' can enhance the provision of ecosystem services, simply because the presence of more
55 species increases the likelihood that an ecosystem will contain a species that grows faster, is more
56 resistant to a particular disturbance, or has some other advantageous trait that leads to enhanced
57 ecosystem functioning or provision of services, compared to communities with fewer species (Wardle
58 2001; Lefcheck et al. 2015).

59
60 Given the role of biodiversity in the provision of ecosystem services, the widespread degradation of
61 forests is likely to have far-reaching effects, such as reduced resistance (or increased susceptibility) to
62 natural or anthropogenic disturbance. As such disturbances appear to be increasing in frequency and
63 intensity (e.g., Pachauri et al. 2014, Brockerhoff and Liebhold 2017, Freer-Smith and Webber 2017)
64 declines in biodiversity are likely to reduce forests' resistance to climate extremes (e.g., Isbell et al.
65 2015) and to pests, pathogens, invasive species, and other disturbance factors (e.g., Jactel et al. 2017),
66 and to reduce the provision of ecosystem services in general (e.g., Vilà and Hulme 2016).

67
68 Compared with 'natural forests' or mixed-species forests, planted forests usually have a lower level of
69 biodiversity of canopy trees and other species (e.g., Barlow et al. 2007, Brockerhoff et al. 2008), and it is
70 likely that their ability to provide certain ecosystem services is reduced. For example, mixed forests tend

71 to be more effective in delivering a range of provisioning services (e.g., Gamfeldt et al. 2013; Forrester
72 and Bauhus 2016), and are more resistant to various disturbances than single-species planted forests
73 (Jactel et al. 2017). These relationships between forest type, biodiversity and ecosystem services are
74 highly relevant for informing forest policy and management. However, given the multitude of ecosystem
75 services, it is difficult to generalise about the role of forest diversity. Furthermore, there are trade-offs
76 between different ecosystem services depending on the tree mixture and stand type involved. Some
77 tree mixtures are superior at providing certain services but other tree mixtures or even single-species
78 forests are more effective for other services (e.g., van der Plas et al. 2016a).

79
80 There has been much progress recently in this very active field of research, and the International Union
81 of Forest Research Organisations (IUFRO) established a task force to facilitate multi-disciplinary research
82 collaboration and literature reviews on the effects of forest biodiversity on single and multiple
83 ecosystem services. The current paper provides a general literature review on this topic and serves as an
84 introduction to a special issue consisting of 10 papers on various aspects of forest biodiversity,
85 ecosystem services and related issues. Habitat provision is a central theme for several contributions. A
86 review of analytical methods using readily-available forest inventory data for biodiversity assessments is
87 provided by Corona et al. (2017). The effects of afforestation of open land on bird communities and
88 biodiversity in Ireland and Argentina are examined by Graham et al. (2017) and Phifer et al. (2017),
89 respectively, highlighting the importance of considering the previous land use context. For example,
90 while afforestation of Irish peatlands and grasslands of high conservation value was considered
91 detrimental for bird biodiversity, in the case of intensively managed grassland, afforestation can lead to
92 higher densities of bird species of conservation concern (Graham et al. 2017). Such nuanced
93 observations are particularly important in areas that have experienced severe deforestation
94 (Brockerhoff et al. 2008), such as Ireland where only 1% of the land area remains in natural woodland
95 (O'Callaghan et al. 2017). Under such circumstances, even plantations of exotic trees can provide
96 important habitats for forest species, although attention needs to be given to management options that
97 enhance the value for forest specialists and species of conservation concern (O'Callaghan et al. 2017).
98 The maintenance of ecosystem services provided by aquatic biota in managed forests in north-western
99 North America is examined by Penaluna et al. (2017). They highlight the complex nature of relationships
100 between aquatic biodiversity and numerous ecosystem services and the need for better quantification
101 and understanding of process interactions. Pollination of crop plants and wild plants is an important
102 ecosystem service worldwide. Taki et al. (2017) explore the use of stable isotope analysis to investigate
103 how land use and climate affect wild bee populations. This provides a useful approach for the study of
104 relationships between biodiversity, land use and the provision of pollination services. The effects of
105 invasions of tree pests and pathogens on forest biodiversity and ecosystem services are assessed by

106 Freer-Smith and Webber (2017), highlighting the urgent need to mitigate the risk of future invasions and
107 to increase our ability to manage those that have already occurred. Cultural ecosystem services are
108 highly relevant in indigenous communities. Lyver et al. (2017) use interviews with members of an
109 indigenous tribe in New Zealand that has strong connections with the surrounding forest to assess
110 temporal changes in forest use and perceptions of forest health. Finally, Vangansbeke et al. (2017)
111 examine trade-offs between biodiversity, wood production and recreation in planted pine forests and
112 how forest management planning can be optimised spatially to integrate the delivery of multiple
113 ecosystem services.

114
115 The objectives of this paper are to: (1) provide an overview of the various 'ecosystem services' that are
116 provided by forests; (2) clarify the definitions of ecological processes, ecosystem function, and
117 ecosystem services and goods; and (3) review and synthesise the current state of knowledge regarding
118 forest ecosystem services and the role of forest biodiversity in the provision of these ecosystem
119 services.

120
121

122 **Ecosystem processes, functions, services are distinct concepts**

123
124 It is widely recognized that biodiversity is a major driving force in ecosystem function (Hooper et al.
125 2005; Schulze and Mooney 2012). Hundreds of studies have addressed the effects of tree species
126 diversity on many forest ecosystem functions, including primary production (e.g., Liang et al. 2016). In
127 this very active field of research, the statement that tree diversity can improve "forest ecosystem
128 function and (associated) services" has become very common. However, the concepts of ecosystem
129 function and ecosystem services are often confused, even though they are different in terms of their
130 definition and relevance to scientists and managers. Whereas "function" is an ecosystem-centred
131 concept, "ecosystem service" is human-centred (see **Box 1** for definitions and an example). Focusing on
132 function allows scientists to understand how changes in forest biodiversity can modify the key ecological
133 processes that are driving the functioning, integrity or maintenance of forest ecosystems. Given the
134 linkages and relationships between ecosystem functions and services, forest managers or policy makers
135 may use such information to predict how biodiversity management or enhancement can affect the
136 delivery of goods and services beneficial to the economy and to human well-being.

137

138 **Insert Box 1 about here**

139

140 Forests generally are well-placed to deliver most of the ecosystem services (ESs) listed in current
141 frameworks such as the Millennium Ecosystem Assessment (Millennium Ecosystem Assessment 2005) or
142 CICES (CICES 2013), because of their wide distribution, rich biodiversity and long history of human use
143 (see **Table 1** for an overview of ESs relevant to forest ecosystems). However, empirical studies that
144 establish quantitative and causal relationships between forest biodiversity and ecosystem services are
145 lacking for many important ESs (Mori et al. 2017). For example, focusing only on the effect of tree
146 species diversity, we found that the number of published articles (see **Online Resource 1** for details on
147 the methodology) addressing ESs provided by mixed forests was highly skewed towards provisioning
148 services, particularly the provision of wood biomass, and regulating services such as the regulation of
149 pests and diseases (**Figure 1**). The provisioning of nutrition and energy services, and the cultural services
150 delivered by mixed-species forests, are largely under-represented in the literature.

151

152

153 **Tree diversity effects on biomass production**

154

155 Productivity is often higher in mixtures than in monocultures, and this effect can increase with tree-
156 species richness (Forrester and Bauhus 2016; Liang et al. 2016). A recent global meta-analysis of
157 mixture-monoculture comparisons found that the productivity of mixtures was, on average, 26.5%
158 greater than the mean of the respective monocultures (i.e., overyielding) and 9.8% greater than the
159 most productive of the respective monocultures (i.e., transgressive overyielding) (this excludes very
160 young mixtures where the effects were smaller) (Gritti et al., cited in Pretzsch and Forrester 2017).
161 However, while productivity has often been found to increase along gradients of increasing tree-species
162 richness, there are also instances where there is no increase, or even a decrease in productivity
163 (Forrester and Bauhus 2016). Even when there is an increase in growth with increasing tree-species
164 richness, it does not mean that the mixtures are always more productive than all the monocultures; it
165 only indicates that the mean productivity of a given diversity level is greater than the mean productivity
166 of a lower diversity level, such as the monocultures. Therefore increasing tree-species richness within a
167 given stand will not necessarily result in greater productivity. This would require that the species
168 interact in complementary ways, and therefore when considering specific stands (as opposed to regional
169 patterns), species identity is likely to be more important to consider than species diversity *per se*.

170

171 Positive mixing effects, or complementarity effects, can result from many different processes and
172 species interactions. These have been the subject of several reviews (Kelty 1992; Richards et al. 2010;
173 Forrester and Bauhus 2016) and can be described as nutrient-related, water-related or light-related
174 interactions in addition to biotic interactions (e.g., reduced pest damage) (Forrester and Bauhus 2016).

175 Examples of nutrient-related processes are symbiotic nitrogen fixation and accelerated rates of nutrient
176 cycling, or where the abundance and composition of mycorrhizae change under mixtures leading to
177 greater the uptake of different forms of a given nutrient (Lovelock and Ewel 2005; Richards et al. 2010).
178 Water-related interactions include differences in rainfall interception by the canopy, transpiration,
179 water infiltration or storage in the O horizon and hydraulic redistribution. Light-related interactions
180 include differences in crown architecture and canopy structure that influence light absorption, or
181 differences in physiology or phenology that influence the efficiency of light use and the timing of light
182 absorption.

183
184 Many of these processes or interactions are related to stand structure or tree architecture, rather than
185 tree species diversity *per se*. This is the case for most light-related interactions, many water-related
186 interactions and a small proportion of the nutrient-related interactions (Forrester and Bauhus 2016).
187 This suggests that many of these processes and interactions could be important in monocultures that
188 are heterogeneous, especially uneven-aged monocultures. However, just as tree species diversity does
189 not necessarily increase productivity, structural diversity has also been found to have negative effects
190 on productivity, and in some forest types increasing size heterogeneity can reduce productivity by 20%
191 (Binkley et al. 2010; Ryan et al. 2010; Stape et al. 2010; Aspinwall et al. 2011; Luu et al. 2013; Bourdier et
192 al. 2016; Soares et al. 2016). In such stands, the heterogeneous size structure enables larger trees to
193 acquire higher quantities of a given resource than smaller trees, which they also use more efficiently
194 than smaller trees. The smaller trees acquire fewer resources and use them less efficiently, which has a
195 greater negative effect on stand growth than the positive effect experienced by the larger trees (Binkley
196 et al. 2010).

197
198 Mixing effects for any given species composition will often change along spatial or temporal gradients of
199 resource availability or climatic conditions. In general, complementarity for a given species has been
200 found to increase as the availability of resource “A” declines (or climatic condition A becomes harsher) if
201 the species interactions improve the availability, uptake, or use efficiency of resource A (or interactions
202 improve climatic condition A) (Forrester and Bauhus 2016). If soil nitrogen availability is high then any
203 nitrogen fixed by a nitrogen-fixing species is unlikely to have much of an effect on non-nitrogen-fixing
204 species (Forrester 2014). For example, the growth of *Pseudotsuga menziesii* was greater when it was
205 mixed with the N-fixing *Alnus rubra* on a low-N site, but not on a high-N site (Binkley 2003) (**Figure 2a**).
206 The complementarity effect was as high as 100% and was related to greater nutrient uptake rather than
207 changes in nutrient availability or nutrient-use efficiency. The rates of N, Mg and K uptake were greater
208 in mixtures than in *P. menziesii* monocultures at both sites, but the relative increases were much greater
209 at the low N site (Binkley et al. 1992). The same pattern can be expected for water- and light-related

210 interactions along gradients in water status or gradients in light competition, respectively (Forrester
211 2014). For example, the drought sensitivity (%) of *A. alba* was reduced when mixed with *P. abies* but
212 only on dry sites (**Figure 2b**; Lebourgeois et al. 2013). It was suggested that this resulted in species
213 interactions that reduced competition for water, which was expected to be more useful on drier sites or
214 during drier periods. In mixtures where complementarity increases as growing conditions improve,
215 interactions that improve light absorption or light-use efficiency may be important. On sites with high
216 nutrient and water availability, stands can develop large leaf areas and competition for light may be
217 intense. Therefore, interactions that improve light absorption or light-use efficiency can be more useful.
218 This was suggested to have caused the increasing complementarity effect for *P. abies* when it was mixed
219 with *A. alba* (**Figure 2c**).

220
221 In conclusion, many studies have identified the processes and interactions that cause mixing effects, and
222 much recent attention has been given to the spatial and temporal dynamics of these interactions
223 because such information is required for most practical applications of mixtures. Important next steps
224 are to determine when and where each individual process or interaction is likely to have the greatest
225 effect on growth or other forest functions and whether certain processes or interactions tend to have
226 the largest effects. This could be combined with analyses of forest inventory data to provide regionally
227 validated information across large spatial and temporal gradients (Forrester and Bauhus 2016). Such a
228 process-based approach could benefit from being combined with modelling studies, which can
229 summarize much of this information while simultaneously making it readily available to foresters
230 (Forrester et al. 2017).

231

232

233 **Habitat provisioning and effects of forest type, structure and diversity**

234

235 Globally, forest specialist species are in decline (e.g., Gregory et al. 2007), particularly those associated
236 with primary forests containing old trees and biological legacies. There is an urgent need to identify the
237 impacts of management on habitat provisioning in forest ecosystems and to highlight potential
238 mitigation measures so that the range of ecosystem functions and services directly supported by
239 biodiversity are maintained.

240

241 Most forest biota respond negatively to forest degradation and to fragmentation from pristine primary
242 forests to small fragmented remnants. Some forest specialists tend to be more sensitive and also
243 respond negatively to habitat conversion from native to exotic plantation forest (Farwig et al. 2008;
244 Irwin et al. 2014; Lindenmayer et al. 2015). However, the relative habitat value of plantation forests

245 depends upon the forest history and context within a region (e.g., Neumann et al. 2017). For example, in
246 countries that are dominated by agricultural landscapes, exotic plantation forests may play a significant
247 role in supporting forest biodiversity by allowing native forest specialists to use an otherwise unsuitable
248 non-wooded landscape matrix (Berndt et al. 2008; Ruffell et al. 2017; O'Callaghan et al. 2017).
249 Nonetheless, increasing fragmentation and loss of primary forest fundamentally alters both the species
250 and functional composition of forested landscapes (Lindenmayer and Franklin 2002; Barnes et al. 2017).
251

252 *Habitat provisioning across forested landscapes*

253 In fragmented forest landscapes the levels of isolation and connectivity are important factors
254 determining habitat provisioning at this scale (Fahrig 2003). For instance, species with poor dispersal
255 abilities, such as epiphytic lichens or small arboreal rodents, suffer significant declines in fragmented
256 landscapes (Jönsson et al. 2017; Santaniello et al. 2017; Linnell et al. 2017), while the diversity of forest
257 specialist plants in plantation forests is positively influenced by proximity to natural woodland patches
258 providing opportunities for colonisation (Coote et al. 2013). Similarly, the amount of natural forest
259 strongly influences the distribution of birds and bats because it provides a significant part of foraging
260 and roosting requirements at the landscape scale (Burgar et al. 2015; Lindenmayer et al. 2015). Further,
261 features such as hedgerows and shrubland patches form important habitat linkages facilitating
262 movement between patches for forest invertebrates such as spiders (Oxbrough et al. 2007). By contrast,
263 birds and bats that use both forest and non-forest habitats benefit from fragmented mosaic landscapes,
264 and forest patchiness is a key landscape-scale resource for such species (Barbaro et al. 2012;
265 Charbonnier et al. 2016). However, the quality of the landscape matrix itself has an effect on native bird
266 distribution at the landscape scale, by mitigating or accelerating declines in bird species richness with
267 increasing native habitat loss when the matrix is dominated by either wooded or non-wooded exotic
268 habitats (Deconchat et al. 2009; Ruffell et al. 2017). Forest harvesting and the resulting interspersions of
269 complementary habitats in the landscape mosaic is also critical to large herbivorous mammals, providing
270 both cover and foraging areas (Côté et al. 2004; Nikula et al. 2004). However, large-scale habitat
271 provisioning by mature and intact forests is vital for many declining forest specialists as well as for the
272 conservation of functionally diverse forest taxa assemblages (Lindenmayer and Franklin 2002; Irwin et
273 al. 2014).

274

275 *Habitat provisioning at within- and between-stands scales*

276 Large-scale forest management can lead to biotic homogenization of forest environments at stand and
277 landscape scales; for example, when multispecies landscapes are replaced by even-aged monocultures,
278 although in boreal forests the opposite effect may also occur. Diversification of tree species or age
279 ranges either between stands in a forested landscape or within stands at a smaller scale generally

280 enhances habitat provision for invertebrates such as arboreal beetles, and for birds and mammals
281 (Nikula et al. 2004; Plath et al. 2012; Styring et al. 2011). Mixtures of conifers and deciduous trees may
282 enhance biodiversity by providing habitats suitable for species associated with different tree species. For
283 example, such mixtures may lead to greater bat species diversity through increased habitat
284 heterogeneity and feeding resources, compared to forest monocultures (Burgar et al. 2015; Charbonnier
285 et al. 2016). Invertebrates (e.g., spiders and beetles) and plants tend to respond more to small-scale
286 structural changes associated with the presence of individual tree species driven by light availability and
287 litter inputs (Chavez & MacDonald 2012; Oxbrough et al. 2016).

288
289 Diversification of age structures provides habitats for the range of species associated with each stage of
290 the successional forest cycle and is a key driver of biodiversity. However, in tropical forests, gap-phase
291 dynamics tend to be more important than successional cycling. Together with tree composition, stand
292 stratification and age structure are important drivers of bat and bird diversity in forests because they
293 directly affect their foraging (Barbaro et al. 2012; Jung et al. 2012; Phifer et al. 2017) whereas
294 invertebrates, bryophytes and vascular plants respond more to changes in forest structure and light
295 levels (Smith et al. 2008). Late successional stages have significant conservation importance due to their
296 structural diversity and widespread rarity in the landscape (Lindenmayer 2017), whereas in regions that
297 have experienced substantial loss of natural forest cover, older plantation forests can play an important
298 role in supporting a range of native forest species (Berndt et al. 2008; Deconchat et al. 2009; Irwin et al.
299 2014; Ruffell et al. 2017). Primary forest and older stands provide important biological features such as
300 habitats for flora and fauna associated with large or late successional tree species, a greater diversity of
301 deadwood or more diverse stand structures (e.g., Burgar et al. 2015; Lindenmayer 2017; Linnell et al.
302 2017). However, forest ecosystems provide habitats for differing suites of species at each stage of the
303 forest cycle. For instance, at the early stages of tree establishment a range of open habitat and
304 generalist invertebrate and plant species coexist (Smith et al. 2008), a role which may be important in
305 landscapes dominated by intensive agriculture with low overall biodiversity (O'Callaghan et al. 2017).
306 Large herbivorous mammals such as moose (*Alces alces*) select early successional forest stages due to
307 the availability of food resources during winter (Nikula et al. 2004), as do hen harriers (*Circus cyaneus*),
308 since such habitats provide suitable ground nesting sites and an abundance of small mammalian prey
309 (Wilson et al. 2009). Further, modern silvicultural practices such as tree planting after logging have
310 considerably improved habitat quality for deer. Increased plant diversity provides abundant and high-
311 quality food resources, and this contributes to problems from an overabundance of deer in many
312 regions (Côté et al. 2004).

313

314 Deadwood is a significant contributor to habitat provision in forest ecosystems and is recognised
315 internationally as an indicator of forest health. Deadwood tends to be more abundant in old growth or
316 less managed stands (except in tropical forests) and provides both habitat and forage for a large suite of
317 the forest biota (Seibold et al. 2015). Many forest bird and mammal species depend on the presence of
318 tree cavities associated with deadwood for nesting and roosting (Cockle et al. 2011; Burgar et al. 2015).
319 Saproxylic fungi, plants and invertebrates respond to changes in deadwood characteristics including
320 volume, size classes, situation and decay stage, which provide variety in habitat structure and available
321 food sources at differing stages of the decomposition process (Seibold et al. 2015). For instance, wood-
322 boring invertebrates may initially colonise early decay stage wood, providing mechanisms for fungi to
323 enter and enhance the decomposition process for later successional species (Ulyshen 2016).

324

325 *Knowledge gaps and future challenges*

326 Forest ecosystems support a large proportion of species threatened with extinction, and more applied
327 research is urgently needed to evaluate sustainable forest management practices that will contribute to
328 the protection of threatened species. The diversity of forest structure and composition need to be
329 maintained at landscape and regional scales as a spatial insurance to provide habitats for a large suite of
330 specialist forest species. Habitat provisioning by forests for multiple taxa and trophic levels is a key
331 ecosystem service, which in turn positively influences forest ecosystem functioning through a range of
332 mechanisms (Barnes et al. 2017; Lindenmayer 2017). There is also a need for increased public and
333 political support for sustainable forest management to reduce species losses. The impacts of large-scale
334 forest harvesting, thinning and replanting with exotic species on habitat provisioning on well-known
335 groups of mammals, birds and plants are relatively well-investigated using basic community-level
336 metrics (e.g., species richness, abundance, species composition). However, for less charismatic groups
337 such as some invertebrates and fungi, and for more complex community interactions and ecosystem
338 functions, as well as longer-term impacts like climate change, the effects of forest management and
339 mitigation measures remain largely unknown and present a significant future research challenge. This is
340 particularly relevant for the biota associated with forest canopies and the flora and fauna of tropical
341 forests, where the impacts of forest fragmentation and modern forest practices remain largely unknown
342 despite these forests' high conservation value and their considerable role in the provision of ecosystem
343 services.

344

345

346 **Pollination and forest diversity**

347

348 Animal pollination, which is fundamental to the reproduction and persistence of most flowering plants,
349 is an important ecosystem service (Millennium Ecosystem Assessment 2005). As biodiversity contributes
350 to various ecosystem processes, functions and services, the declining diversity and abundance of
351 pollinators (mainly insects and birds) has raised concerns about the effects on both wild and crop plants
352 (Potts et al. 2010). Experimental evidence indicates that greater pollinator diversity results in improved
353 seed production in plants (Fründ et al. 2013). Furthermore, it has also been shown that pollinator
354 species richness *per se* is not as important as the diversity and complementarity of functional traits of
355 pollinators, such as different plant species and ambient temperature preferences (Fründ et al. 2013).

356
357 In agricultural ecosystems, pollination services are provided by numerous species of wild insects and
358 vertebrates, as well as some managed species that also rely on wild ecosystems for nesting and food
359 resources (Garibaldi et al. 2013). Approximately 75% of the world's leading food crops, such as cacao
360 and oil palm in the tropics and almonds and apples in temperate regions, depend at least in part on
361 animal pollination for yield and/or quality (Klein et al. 2007). The economic contribution to the current
362 global crop production attributed to animal pollination is estimated to have an annual market value
363 ranging between US\$235 billion and US\$577 billion (Potts et al. 2016). Diversified farming systems such
364 as mosaic agricultural landscapes with forest remnants and agroforestry are more effective than large
365 agricultural monocultures in providing nesting and floral resources for pollinators and in sustaining
366 pollinator populations and communities throughout the year (Fahrig et al. 2015). The conservation of
367 natural ecosystems such as forests, which may provide habitats for pollinators, is crucial, and the
368 distance from these habitats to farms affects the success of seed and fruit set (Kennedy et al. 2013).

369
370 In terrestrial ecosystems other than agricultural systems, it is estimated that over 85% of wild flowering
371 plants globally are reliant to some degree on animals to transfer pollen (Ollerton et al. 2011). The wide
372 variety of pollinator species contributes to the successful pollination of wild plants, and many flowering
373 plants and their pollinators have close co-evolved relationships (Proctor et al. 1996). Greater diversity of
374 pollinator species and functional groups generally enhances the success of pollination services
375 (Tylianakis et al. 2008). Local pollinator loss can be a serious threat to plants that are dependent on
376 certain pollinators, potentially causing their eventual extinction. Empirical studies in forest landscapes
377 showed negative correlations between pollination success in wild plants and the extent of loss and
378 fragmentation of forest remnants (Aizen and Feinsinger 1994). Although the economic value of
379 pollination of wild plant species has not been quantified, it is certain that it contributes substantially to
380 the provision of food, habitats and other resources for a wide range of organisms.

381

382 Tree types and human management of forests affect pollinators and pollination services. Planted forests
383 that consist of one tree species, grown as even-aged monocultures and intensively managed, may result
384 in reduced diversity and abundance of pollinators compared with natural forests that have greater
385 structural and plant species diversity (Taki et al. 2011). However, there are cases where active
386 management of planted forests results in positive effects on pollinators. For example, thinning trees
387 may enhance the diversity and abundance of pollinators in planted forests (Taki et al. 2010). Even clear
388 cutting and other disturbances of planted forest that create open environments that are preferred by
389 early successional species that can act as pollinators (Rubene et al. 2015; Taki et al. 2013). Moderate
390 levels of human disturbance of forest ecosystems and anthropogenic land use may result in greater bee
391 abundance and species richness (Winfree et al. 2007). However, some pollinator species such as
392 honeybees and stingless bees use old growth forest for nesting in cavities in large trees (Michener
393 2007).

394
395 Maintaining the quantity and quality of natural or semi-natural forest ecosystems across the landscape
396 is important to conserve and restore habitats for pollinators. Retaining habitats within a landscape helps
397 to safeguard an essential level of pollination services for both agricultural and forest ecosystems.
398 Beyond the landscape scale, habitat conservation and restoration at the local scale are also necessary to
399 provide nesting and feeding resources for pollinators (Taki et al. 2017). However, there are still gaps in
400 our knowledge about how landscape and local scale management of forested ecosystems can be
401 integrated for the best outcome for pollinators and pollination services.

402

403

404 **Biodiversity and seed dispersal**

405

406 Seed dispersal by mammals is a major factor in maintaining tree community structure over the long
407 term in tropical forests (Seidler and Plotkin 2006) and is a key mechanism that explains the pattern of
408 low aggregation of conspecifics on tropical forest plots. Evidence also suggests that tropical forests
409 deprived of seed-dispersing animals exhibit replacement of fruiting trees by species with wind seed
410 dispersal (Brodie and Aslan 2012). While the seeds of many tree species are dispersed by wind, others
411 are dispersed by herbivores and frugivores (a process known as zoochory), especially in tropical forests.
412 In Mexico, Cortes-Flores et al. (2013) found that 68% of tree species were dispersed through zoochory.
413 Reduced or absent populations of seed-dispersing animals result in poor to no dispersal, especially of
414 large-seeded trees that depend on large animals such as elephants (Anzures-Dadda et al. 2011; Brodie
415 and Aslan 2012; Beaune et al. 2013). Some animal species play important co-evolved and
416 complementary roles in maintaining plant communities (Gonzalez et al. 2009; Garcia and Martinez 2012;

417 Gonzalez-Varo et al. 2013). The rate of seed germination for some species is enhanced by passage of
418 seeds through mammalian guts (endozoochory) (Traveset 1998; Campos-Arceiz and Blake 2011).
419 Absence of dispersal processes results in a homogenisation of forest plant species and has long-term
420 consequences for forest structure and other ecosystem services (Terborgh et al. 2008; Lehouck et al.
421 2009; Markl et al. 2012). Proximity of seed sources affects seed dispersal processes to adjacent areas, so
422 habitat connectivity can improve the influx of animal-dispersed seeds (Lehouck et al. 2009; Jesus et al.
423 2012). Animal species that simply drop seeds have effective distances of generally under 0.5 km
424 (Wehncke and Dominguez 2007) but dispersal distances by seed-eaters are often many kilometres
425 (Beaune et al. 2013). Hence, the loss of seed dispersers and their habitats ultimately produces a decline
426 in local or regional tree species richness (Lehouck et al. 2009; Beaune et al. 2013; Bueno et al. 2013).

427

428

429 **Resistance to wind storms**

430

431 Wind is a major disturbance agent in all forests (Payn et al. 2015) and a key part of the dynamics of
432 many natural forest ecosystems, particularly temperate forests (Ulanova 2000; Wolf et al. 2004).
433 However, wind damage can have large economic, environmental and social impacts on managed forests
434 and the societies that depend on them (Gardiner et al. 2013). Therefore, mitigating the impact of wind
435 damage in such forests is a way to help maintain the important ecosystem services that managed
436 forests can provide to society.

437

438 Natural forests are remarkably resilient to major damaging events such as storms and hurricanes
439 (Cooper-Ellis et al. 1999) and it is possible that the mixed structure and mixed species of such forests
440 contribute to both their resistance and resilience. However, very little is known about the processes
441 involved in wind damage and recovery in natural forests and it has proven necessary to investigate the
442 behaviour of managed forests to understand the functioning of natural forests in response to wind
443 damage (Everham III and Brokaw 1996). For example, there is evidence that wind damage to managed
444 forests can be reduced by the use of multiple species and variable forest structures, for a number of
445 reasons. Firstly, there are differences between species in the level of resistance to wind damage
446 (Hanewinkel et al. 2013) and the overall stability of a forest can be enhanced by using more resistant
447 species to provide a framework. Secondly, more stable species can help stop damage propagation
448 during a storm, which occurs when an unstable or weak tree is damaged and creates a gap in the forest,
449 increasing the wind loading on the remaining trees and leading to further damage (Dupont et al. 2015).
450 Thirdly, in systems with a mixture of species, the slower growing species may die and act as a self-
451 thinning system that removes the dangers of normal thinning where the canopy is opened up and

452 increases the wind loading on the remaining trees (Quine and Malcolm 2007). Fourthly, there is
453 evidence that wind loading on broadleaves is reduced in the winter, which is the period with the
454 strongest winds, because they lose their leaves and have reduced overall drag (Bonnesoeur 2016), so an
455 admixture of broadleaves could be beneficial to overall stand stability. Fifthly, when the canopy is multi-
456 storied because of age and species variation, the momentum absorption from the wind appears to take
457 place over a greater depth of the canopy and measurably reduces the wind loading on the tallest trees
458 (Gardiner et al. 2005). Finally, multi-storied forests are less at risk following harvesting of the tallest
459 trees, for example, in a single-tree selection system, or if individual trees start to blow down in a storm,
460 because the under-storey trees are smaller and will experience lower wind loading even when gaps are
461 created.

462
463 Based on the discussion above it is probable that natural forests are more resistant and more resilient to
464 wind damage because of their mixed structure due to variations in age and species. Therefore, managed
465 forests that more closely mimic natural forests are almost certainly more resilient than even-aged
466 stands, will recover more quickly after a damaging event, and ecosystem services from the forest will be
467 restored more rapidly. In addition, mixed species and age stands will require less technical and financial
468 input to recover after storm damage (Stanturf et al. 2007) because the understory trees will be able to
469 grow into the space previously occupied by the damaged trees and less intervention will be required.
470 Therefore, by having a mixture of species and tree ages it is possible to have a forest with high
471 biodiversity and compositional structure, as well as one that is more resistant and resilient to wind
472 disturbance. However, it must be remembered that resilience in forests is a dynamic process, and
473 following a large wind disturbance a forest will be different and so will be the level of ecosystem
474 services it can provide.

475

476

477 **Fire regulation and mitigation**

478

479 Fire is an essential process in the natural dynamics of some ecosystems, and a potential selection force
480 behind the current distribution of vegetation types worldwide (Bond and Keeley 2005). Although fire
481 can diminish the well-being of people and drastically reduce ecosystem services, fire is a natural process
482 in many ecosystems, and it is not necessarily a negative element *per se*. The maintenance of a natural
483 fire regime is often required to sustain or even enhance the productivity of ecosystems that have
484 coexisted, or even coevolved, with a specific fire regime (Brockway et al. 2002). Therefore, the impact of
485 fire on a forest and its associated ecosystem services can be either positive or negative, depending on
486 the forest type, the fire regime, and the ecosystem services (Thom and Seidl 2016).

487
488 However, it is also recognized that global change (climate change, population growth, change in land
489 use practices, or even an increase in fire suppression efforts) has modified fire regimes worldwide,
490 causing an increase in the frequency of large catastrophic fires and an associated decrease in the supply
491 of ecosystem services (Schröter et al. 2005). In addition to the negative influence of large fires on a
492 number of ecosystem services, such fires also have a direct and negative impact on the well-being of
493 humans, due to air pollution, cost of suppression activities, and loss of property and human lives. In this
494 context, fire risk mitigation, aiming to reduce the frequency and impact of catastrophic fires, and fire
495 regulation to maintain a desirable fire regime, can be considered ecosystem services themselves.

496
497 Fire regulation and mitigation require the maintenance of a certain fuel load and spatial continuity of
498 fuels, using active management to reduce the risk that fire can impose on ecosystem services, while
499 maintaining those ecosystem processes and services that depend on fire (Sturtervant et al. 2009). In this
500 sense, forest biodiversity is often overlooked, unless one considers the clearance of trees and shrubs in
501 the lower forest strata to mitigate fire risk as a strategy that influences biodiversity. Even though the
502 impact of fire on biodiversity, either positive or negative, has been frequently addressed, the impact of
503 species diversity on fire mitigation and regulation is usually neglected.

504
505 It is assumed that a diverse landscape will help to modify fire behavior, minimize negative impact, and
506 create more resistant and resilient landscapes and ecosystems (Fernandes et al. 2010). However, what
507 applies to large-scale landscapes is not always true at the stand level. When considering the impact of
508 increasing diversity on fire behavior and forest resistance, we have to assume that individual trees'
509 resistance to or survival capacity in a fire of a given intensity and duration depends on the capacity of
510 each tree to protect sensitive tissues (Dickinson and Johnson 2004). This capacity is defined by each
511 tree's size and species. Mixing the right set of species in a stand may have a positive impact on tree
512 growth – one of the desirable traits for resisting fires – but may also result in more continuous fuel
513 supplies, leading to more intense fires. The limited number of studies that have analysed the impact of
514 species composition and level of mixture on fire behavior and tree mortality have all identified higher
515 resistance in conifer-broadleaf mixtures compared to pure conifer stands. Forest stands composed of
516 broadleaved trees are usually more resistant to fire, even when pure, mainly due to their lower
517 flammability and their resprouting capacity. Therefore, the impact of increasing species diversity on
518 stand resistance should take into account the capacity of each species to resist fire, and the potential
519 changes in fire behaviour caused by modifications of the forest and the fuel supply structure (González
520 et al. 2006, 2007).

521

522 Reducing fire intensity and increasing forest resistance are, in most cases, achieved by the same
523 management approaches, which aim to reduce the negative impact of fire on most ecosystem services
524 and minimize the direct impact of fire on human well-being. However, when considering the long-term
525 impact of fire on ecosystem services, the resilience of forest stands cannot be overlooked. Functional
526 traits defining the resistance or resilience of trees to fire are often species-specific (Bond and Midgeley
527 1995), especially in conifers. Mixing species with different traits may limit the resistance of a forest due
528 to changes in fire regimes, but at the same time allow a faster post-fire recovery of the vegetation cover
529 (Martín-Alcón et al. 2015) and the associated ecosystem services.

530
531 In conclusion, the use of forest diversity as a means for fire mitigation and/or regulation needs to
532 consider the spatial nature of fire. Generating a diverse and fragmented landscape, consisting of a
533 mosaic of different forest types and land uses, is a clear strategy for minimizing the negative impacts of
534 fire, inside and outside the forest. However, selecting a forest typology for mitigating fire is not a
535 straightforward decision at the stand level. Any decision regarding forest composition and management
536 should consider the fire regime (real or emulated) that is expected or will be regulated. It should also
537 consider the response of the tree species to such fire regimes, according to their functional traits, and in
538 the case of mixtures, the compatibility between species and traits. Finally, trade-offs between responses
539 to fire and impacts on ecosystem services should be evaluated in order to efficiently manage different
540 forest typologies. In general, the impact of mixing species on a stand's post-fire resistance has been
541 poorly studied, or oversimplified. Past studies are scarce, local, and often based on broad species
542 groupings (such as conifers and broadleaves). Further research is required to identify which species have
543 compatible functional traits for inducing enhanced fire resistance, including an assessment of the
544 combined accumulation and structure of living and dead fuels. Other aspects that call for further
545 research include the impact of mixing species on forest humidity and fuel moisture, and the non-
546 additive effect of mixing different fuels on flammability.

547

548

549 **Effects of forest tree diversity on pest regulation of native and invading insects**

550

551 Insect damage can have major impacts on forest ecosystem functioning (Boyd et al. 2013). For instance,
552 bark beetle outbreaks causing large-scale mortality have been observed to shift forests from carbon sinks
553 to carbon sources (Kurz et al. 2008). Even minor chronic damage such as background defoliation (Kozlov
554 et al. 2015) may result in significant growth loss in trees (Zvereva et al. 2012).

555

556 Although it is a common belief among foresters that forest monocultures are more susceptible to pest
557 outbreaks and insect invasions than mixed forests, it has only recently been demonstrated, via meta-
558 analyses, that tree species grown in pure stands are, on average, significantly more affected by insect
559 herbivory than the same species grown in mixed stands (Jactel and Brockerhoff 2007; Castagneyrol et al.
560 2014a, Guyot et al. 2016; Jactel et al. 2017). This phenomenon has been termed ‘associational resistance’
561 (Barbosa et al. 2009). However, most stand-scale studies involved native insects, and there is
562 comparatively little information on invasions by non-native insects. Two studies in Europe have shown
563 negative relationships between tree species richness and the abundance of invasive tree-feeding insects
564 at the plot or stand scale (Jactel et al. 2006; Guyot et al. 2015). Conversely, in the USA, a positive
565 relationship between native tree species richness and the number of successful invasions by non-native
566 tree-feeding insects was observed (Liebhold et al. 2013), although that study assessed larger-scale county-
567 level data that are not directly comparable with plot-level data.

568
569 While forest insect damage has been found to decrease along gradients of tree diversity in temperate
570 forests (Guyot et al. 2016), tree species composition appears to be more important than tree species
571 richness *per se* in explaining diversity-resistance relationships in forest ecosystems. In particular, the
572 likelihood of associational resistance increases with the functional dissimilarity of associated trees in
573 mixed forests (Castagneyrol et al. 2014a). This would explain why there is weak evidence for better
574 resistance of pure stands composed of several genotypes of the same species compared to single-
575 genotype monocultures (Moreira et al. 2014, Barton et al. 2015).

576
577 Three main ecological mechanisms are proposed to explain why pest regulation is more effective in mixed
578 forests. The first mechanism relates to the density of host trees, which is proportionally reduced in forests
579 where host and non-host species are ‘associated’ compared to pure forests of host trees. The resource
580 concentration hypothesis (Root 1973) predicts that herbivores are less likely to find, remain and feed on
581 their host trees when they are less numerous and scattered amongst non-host trees in mixed stands
582 (Sholes 2008). This mechanism mainly occurs at the patch (‘stand’) level (Hambäck and Englund 2005),
583 depending on the ability of herbivores to perceive the overall quality of the patch, thus influencing patch
584 immigration and residence rates (Verschut et al. 2016).

585
586 The second mechanism relates to the ability to locate and exploit individual host trees, depending on the
587 frequency and identity of host and non-host trees. Non-host trees may reduce the visual apparency
588 (Castagneyrol et al. 2014b) and chemical apparency (Jactel et al. 2011) of host trees, making them more
589 difficult for insects to find. Neighbouring trees from other, associated species may also be preferred by
590 insect herbivores, leading to a diversion process that benefits the focal tree species (Jactel et al. 2005).

591 This mechanism thus occurs within a patch (or 'stand'), depending on insects' movement between
592 resources, resource perception and dietary preferences (Hambäck and Englund 2005; Verschut et al.
593 2016). Both mechanisms involve plant–herbivore interactions and are more effective against specialist
594 insect herbivores (monophagous) than generalists (polyphagous) (Castagneyrol et al. 2014a). In some
595 cases, generalist pests may even cause more damage in mixed forests (associational susceptibility, e.g.
596 Schuldt et al. 2010) as a result of spill-over onto less preferred neighbouring species after the depletion
597 of the favoured host tree species (White and Whitham 2000), or because of the potential benefits of
598 dietary mixing (Unsicker et al. 2008).

599
600 The third mechanism involves plant–herbivore–predator interactions and is related to the 'enemies
601 hypothesis' (Root 1973). This states that more diverse forests can provide more diverse and abundant
602 feeding and nesting resources for insect predators and parasitoids, thus increasing their capacity to
603 control populations of prey (i.e., insect herbivores). Although an increasing body of evidence supports a
604 positive correlation between tree diversity and natural enemy diversity (Castagneyrol and Jactel 2012;
605 Staab et al. 2014), the actual contribution of predators to the top-down control of pest insects in mixed
606 forests remains difficult to demonstrate (Jactel et al. 2006, Muiruri et al. 2016).

607
608 All three mechanisms are likely to affect non-native invading insects, and they would be expected to
609 mitigate invasions of species-rich forests to some extent. Conversely, because most tree-feeding insects
610 are relatively host-specific, an unavoidable consequence of greater tree diversity is that it leads to an
611 increase in the number of host trees that may be colonised by potential invaders (Liebhold et al. 2013).
612 Ultimately, the extent of realised invasions depends on the combined net effect of negative and positive
613 effects of tree species richness.

614
615 The spatial extent of pest regulation services exhibits a nested pattern. While reduced individual tree
616 damage is probably strongest at the scale of neighbouring trees, for example due to reduced host
617 apparency (Guyot et al. 2015; Damien et al. 2016), improvement of forest health can be achieved at the
618 stand scale (Guyot et al. 2016). Improved effectiveness of biological control by natural enemies may also
619 provide benefits to adjacent land uses such as agricultural crops (Veres et al. 2013).

620
621 The temporal dimension of forest diversity–pest regulation relationships remains the main knowledge
622 gap. On the one hand mixed-forest dynamics are triggered by differences in tree species-specific growth
623 rates, which may lead to changes in host apparency (e.g., Damien et al. 2016) and perhaps host
624 palatability. These factors may change the magnitude and direction of effects on pest insects in the
625 forestry cycle. On the other hand, insect populations have their own dynamics, sometimes with eruptive

626 or cyclic outbreaks, but little is known about whether diversity effects could vary depending on herbivore
627 and predator abundance (Fernandez-Conradi et al. 2017). As a consequence, there is a need for long-term
628 studies testing the influence of tree diversity on the population dynamics of forest insects and estimating
629 the resilience of mixed forests to pest outbreaks.

630
631 The pest regulation service provided by forest biodiversity is thus intimately linked with two main
632 ecosystem functions: primary production (which controls for tree apparency and trade-offs with plant
633 defences) and biotic interactions (e.g., predator-prey interactions). Increasing tree species diversity is
634 likely to result in more complex forest structure and composition, thus providing more habitat for
635 predators and parasitoids that may regulate pest populations through top-down biotic interactions.
636 Bottom-up biotic interactions are also influenced by tree species diversity via both the relative abundance
637 of host vs. non-host tree species for insect herbivores and the diversity of their traits, such as growth
638 pattern and secondary metabolism, which ultimately influence the probability of host trees being found,
639 colonized and damaged (**Table 1**). Pest regulation may have benefits for several forest goods and
640 products. Pest damage reduction ultimately results in more wood biomass of better quality and also helps
641 maintain forest cover, thus regulating air and water quantity and quality, preventing soil erosion, and
642 improving the beauty of forest areas used for recreational activities.

643

644

645 **Biodiversity and carbon sequestration in forests**

646

647 Carbon in forests is sequestered through photosynthesis, and so is directly related to the species level of
648 biodiversity, as follows. Carbon is stored in five distinct pools in forests: above-ground and below-
649 ground live biomass, in deadwood including snags, litter, and soil. Carbon in forests is a function of
650 forest productivity (see above), but the question of the relationship of biodiversity to carbon storage
651 differs somewhat from sequestration. In part this difference occurs because different tree (and plant)
652 species have different wood densities, different rates of photosynthesis and respiration, and because
653 decomposition occurs at different rates, depending on multiple factors. Therefore, in most studies, the
654 functional characteristics and richness of plant communities are major drivers of carbon accumulation in
655 all pools (Kirby and Potvin 2007; Conti and Diaz 2013; Harmon et al. 2013; Lange et al. 2015), although
656 Finegan et al. (2015) found no relationship between species richness and biomass. For soils, Lange et al.
657 (2015) found that elevated carbon storage at sites with high plant diversity is directly related to the soil
658 microbial functional community (i.e., soil biodiversity), which in turn is related to plant species richness,
659 suggesting that soil carbon storage is mainly limited by the integration of new carbon into soil and less
660 by the decomposition of existing soil carbon. In many studies in tropical forests, planted forests and

661 second growth forests – which often lack species with high wood density, and generally have lower
662 taxonomic diversity than primary forests – there is typically lower biomass stored in live and dead
663 biomass pools (Cavanaugh et al. 2014; Gonzalez et al. 2014; Osuri et al. 2014; Shirima et al. 2015). Single
664 species plantations result in reduced litter, or recalcitrant litter, followed by depletion of soil biodiversity
665 and as a consequence less stored soil carbon (de Vries et al. 2013; Zhao et al. 2013; Aslam et al. 2015).

666

667

668 **Cultural ecosystem services in forest ecosystems**

669

670 Cultural ecosystem services (CESs) are defined as ecosystems' contributions to the non-material benefits
671 that arise from complex and dynamic relationships between ecosystems and humans (Chan et al. 2012;
672 Fagerholm et al. 2012). These services are often intangible, making them difficult to measure (Daniel et
673 al. 2012). Commonly recognized CES categories include: cultural diversity and identity, spiritual and
674 religious values; knowledge systems, including education; inspiration; aesthetic values; cultural heritage
675 values; and recreation and ecotourism (Costanza et al. 1997; Millennium Ecosystem Assessment 2005).

676 The emphasis on CES benefits is heavily influenced by a country's cultural, social, economic and political
677 organisation. Populations in societies with access to surplus wealth and leisure time frequently
678 emphasize the importance of aesthetic values, recreation and tourism (Millennium Ecosystem
679 Assessment 2005). In contrast, indigenous peoples often express the importance of CES benefits relating
680 to cultural identity and heritage, kinship, and knowledge integrity and transfer (Pert et al. 2015; Bofo et
681 al. 2016; Sangha and Russell-Smith 2017).

682

683 The global significance of forests to humans means CESs are deeply ingrained in the value-belief systems
684 of many societies. Indigenous forest peoples in particular have a complex matrix of values that shape
685 and guide their attitudes, beliefs and relationships with the forests in which they live (Rickenbach et al.
686 2017). Since the majority of forests worldwide are populated and used by humans (Forest Peoples
687 Programme 2017), the biodiversity contained within these ecosystems contributes extensively to the
688 provision of CES benefits. For example, indigenous peoples commonly link forest landscapes and
689 biodiversity to tribal identities, association with place, kinship ties, customs and protocols, stories, and
690 songs (Gould et al. 2014; Lyver et al. 2017). Spatial patterns of CES identified by rainforest Aboriginal
691 peoples in Australia were related primarily to variations in social structures (e.g., adherence to cultural
692 protocols), rather than to ecological attributes such as forest biodiversity patterns (Pert et al. 2015).

693

694 In developed nations the aesthetic value of forest landscapes has featured strongly in CES assessments
695 of forests. For example, peoples' judgements of scenic beauty in forests of the north-western USA were

696 greater in areas where more green trees were retained by logging companies, provided the retained
697 trees were evenly dispersed across the landscape rather than clumped in small groups (Ribe 2005).
698 Similarly, the Black Wood of Rannoch is one the largest remnants of ancient Caledonian pine forest in
699 Scotland and contributes significant CES values, such as aesthetic and spiritual benefits (Edwards et al.
700 2016). In East Germany, forests are considered a ‘hot-spot’ for CES in regard to education (learning
701 about biodiversity), spirituality and recreation (e.g., hiking – Plieninger et al. 2013). However,
702 biodiversity in these forests also contributes a cultural ecosystem ‘disservice’ as local people have a fear
703 of roaming wolves (Plieninger et al. 2013). Recreation and tourism are by far the most commonly
704 mapped CESs in forest-related assessments, largely because of the ease with which economic-based
705 values can be measured, although estimates can vary widely. An assessment of recreational services
706 provided by forests in North Zealand, Denmark, varied from 5,200 to 14,850 EUR/ha/year for forests
707 with the highest per hectare value, and from 200 to 320 EUR/ha/year for forests with the lowest per
708 hectare value (Zandersen and Termansen 2012). In northern Italy, tourism contributed almost 10% of
709 the total economic value of ecosystem services for the forests of the Fiemma and Fassa Valleys (Häyhä
710 et al. 2015). While recreation and tourism values are critical for many local economies, rising human
711 populations in some countries are increasingly placing pressure on forest resources and the quality of
712 other non-monetary cultural services (Wear and Greis 2002).

713
714 While CESs are a vital part of the ecosystem services complex, they are, on the whole, under-
715 researched. Intangible and non-negotiable CES benefits continue to challenge valuation methods and
716 processes. New valuation tools and frameworks that can reliably account for non-material CES benefits
717 need to be developed and tested. Linking environmental conditions with human wellbeing was a
718 common concept that emerged from the MEA process (Millennium Ecosystem Assessment 2005).
719 Research that explores shared CES concepts between user groups and maps the diversity of CES benefits
720 is therefore needed to assist in conflict resolution (e.g., between tourists and indigenous peoples),
721 especially as activities like recreation and tourism expand globally (e.g., Fagerholm et al. 2012). New
722 frameworks that can consider the full range of CES benefits associated with forest biodiversity will result
723 in solutions and trade-offs for real-world issues to accommodate different sectors of societies. These
724 frameworks can “foster new conceptual links between alternative logics” (i.e., alternative belief
725 systems) “relating to a variety of social and ecological issues” (Milcu et al. 2013). Research that supports
726 the mapping of indigenous peoples’ CES to themes relevant to them will help prevent their values being
727 overlooked or becoming institutionalized in current frameworks.

728

729

730 **Forest biodiversity, multifunctionality and trade-offs among ecosystem services**

731
732 Forests are valued for multiple ecosystem services, including timber production, climate regulation and
733 recreation, and for biodiversity in its own right (Mace et al. 2012). A major challenge for forest managers
734 is to maximise as many of these services as possible, thereby maximising 'ecosystem multifunctionality'
735 (Hector and Bagchi 2007). When different ecosystem services and biodiversity are all positively related
736 to each other, meeting this goal is, at least in theory, relatively straightforward. However, in recent
737 years, a number of studies have investigated relationships between forest ecosystem services and found
738 that while some ecosystem services correlate positively, others show strong negative relationships at
739 local scales (Chhatre and Agrawal 2009; Gamfeldt et al. 2013; Van der Plas et al. 2016a; Lutz et al. 2016)
740 or large spatial scales (van der Plas et al. 2017). Because of these trade-offs, maximising all desired
741 forest ecosystem services is challenging.

742
743 Some trade-offs between ecosystem services occur because different tree species provide different
744 ecosystem functions and services (Gamfeldt et al. 2013; van der Plas et al. 2016a), while others are
745 driven by forest management, which often maximises certain ecosystem services at the cost of others
746 (Chhatre & Agrawal 2009; Verkerk et al. 2014). Hence, at local scales, promoting certain tree
747 communities may maximise some, but not all, ecosystem services of interest. As a result, forest
748 ecosystem multifunctionality generally increases with both tree (Gamfeldt et al. 2013; van der Plas et al.
749 2016a; Ratcliffe et al. 2017) and fungal (Mori et al. 2016) species diversity, although it is almost
750 impossible to maximise all desired ecosystem services and functions underpinning them at local scales
751 (Ratcliffe et al. 2017). Therefore, recent studies have investigated whether larger-scale biodiversity,
752 caused by a high spatial turnover in species composition (i.e. high beta-diversity) can promote
753 ecosystem multifunctionality at the landscape scale. This has turned out to be the case, as a high beta-
754 diversity ensures that different localities complement each other in the ecosystem functions and
755 services they provide (Mori et al. 2016; van der Plas et al. 2016b).

756
757 Because of the large amount of data that is required for research on biodiversity and ecosystem
758 multifunctionality, this field has only taken off relatively recently. Hence, despite many recent advances,
759 there are still many unresolved questions regarding how biodiversity and ecosystem multifunctionality
760 can be simultaneously maximised in natural forests. For example, it is unknown whether the positive
761 effects of local-scale tree species richness on ecosystem multifunctionality are even stronger when co-
762 occurring species differ significantly in their traits or evolutionary origins, although such information can
763 be crucial for planting multifunctional forests. In addition, it is known that forests can provide multiple
764 ecosystem services to neighbouring landscape units, such as agricultural fields (Mitchell et al. 2014).
765 However, whether the benefits of diverse forests for neighbouring fields are greater than those of

766 species-poor forests is still an open question. With the increasing interest in understanding what drives
767 multifunctional landscapes, it is likely that these and other related questions will be investigated in the
768 future.

769
770

771 **Conclusions**

772

773 Our review confirms that forest type and tree species richness affect forest biodiversity and that forest
774 diversity can be an important factor in ecosystem function and the provision of ecosystem services.

775 However, while there are clear mechanisms by which tree diversity can improve ecosystem function and
776 the delivery of ecosystem services, for many ecosystem services, there is still uncertainty about the
777 extent of a ‘functional relationship’ between biodiversity and the provision of those services. We also
778 need to better evaluate the effect of different levels of tree diversity; not only species but also genetic
779 and functional diversity. And while canopy trees are obviously a dominant feature of forests, the
780 diversity of understorey plants, vertebrates, invertebrates, fungi and microbes is also likely to be
781 important for ecosystem services. Furthermore, many ecosystem services remain comparatively poorly
782 studied in forests in relation to biodiversity; this applies particularly to cultural services but also to some
783 provisioning services (see Table 1 and Figure 1). There is clearly a need for more research in this area to
784 enable evidence-based advice for forest management and policy to enhance the provision of ecosystem
785 services (see also Mori et al. 2017).

786

787 For natural forests this discussion may seem somewhat academic, as it is unlikely that tree species
788 composition and diversity would be altered substantially in the interest of ecosystem services.

789 Nevertheless, it is important to raise awareness about the role of natural forests and forest diversity in
790 the provision of ecosystem services to highlight their value beyond the provision of timber and
791 recreation. However, for planted forests there is ample opportunity for optimising their composition
792 and diversity because replanting after harvesting is a recurring process. If it can be shown that there are
793 opportunities for adding value and for increasing the resistance or resilience of planted forests, these
794 should be good incentives for forest owners and managers to consider alternatives to the monoculture
795 paradigm of most planted forests. We thus endorse the plea of Paquette and Messier (2010) “for the
796 implementation of well-conceived, diverse, multi-purpose [forest] plantations as a way to conserve
797 forest biodiversity and ecosystem functions”.

798

799 The relevance of forest ecosystem services does not stop at the forest edge. There is much scope for
800 synergies between forests and farming land uses; for example, even small patches of forest can benefit

801 crop production by enhancing pollinator and natural enemy populations, although they may also
802 provide disservices (Decocq et al. 2016). Adding planted forests to catchments dominated by dairy
803 farming reduces greenhouse gas emissions and improves water quality (Monge et al. 2016). These are
804 also important considerations in the debate about land sharing vs. land sparing. Clearly, any
805 afforestation plans should carefully consider previous land use in terms of the likely biodiversity and
806 conservation outcomes (e.g., afforestation of degraded farmland vs. natural grassland or forest). Finally,
807 any planted forest plan should evaluate options for mixed-species forests (Pretzsch et al. 2017) as these
808 are likely to provide a wider range of ecosystem services.

809

810

811 **Acknowledgements**

812

813 We are indebted to numerous colleagues for invaluable discussions about forest biodiversity and
814 ecosystem services. We thank the International Union of Forest Research Organisations (IUFRO) for
815 facilitating the IUFRO Task Force 'Contribution of Biodiversity to Ecosystem Services in Managed
816 Forests'. Many thanks also to Judy McDonald for edits and comments on the manuscript. EGB
817 acknowledges support from the New Zealand Ministry of Business, Innovation and Employment (MBIE)
818 via core funding to Scion (C04X1104) and contestable funding (C09X1307) to the 'BEST' programme.
819 Contributions by JRG were funded by the Ministerio de Economía, Industria y Competitividad (RYC-2011-
820 08983) and the CERCA Programme / Generalitat de Catalunya. HT was supported by the Ministry of
821 Agriculture, Forestry and Fisheries, Japan, and the Ministry of the Environment, Japan (Environment
822 Research and Technology Development Fund S-15-2).

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1347 **Table 1.** Non-exhaustive list of ecosystem services relevant to forests, based on the CICES classification
 1348 (CICES 2013), and the number of publications related to these ecosystem services that refer to mixed-
 1349 species forests according to the Web of Science (see Online Resource 1 for details)

1350

Section	Division	Class (with examples)	Number of publications
Provisioning	<i>Nutrition</i>	Wild plants (berries, mushrooms) and animals (game) for food	2
		Water for drinking	2
Regulating	<i>Material</i>	Wood biomass (fibres, wood, timber)	416
		Genetic material (for tree breeding)	1
		Water for non-drinking purposes (irrigation)	16
		Fuel-wood	4
	<i>Mediation of toxics or nuisances</i>	Filtration, sequestration (by trees or forest soils, of pollutants)	24
		Mediation of smell, noise, visual impacts (visual screening, noise reduction by trees)	2
	<i>Mediation of flows</i>	Protection against erosion (landslide, avalanches)	63
		Water flow maintenance (precipitation interception)	30
		Protection against flood (by riparian forests or mangroves)	1
		Protection against storms (shelter belts)	17
		Pollination and seed dispersal (by pollinators or seed dispersal forest species)	111
	<i>Maintenance of physical, chemical and biological conditions</i>	Habitat provision (habitat for endangered biota) <i>i.e.</i> biodiversity for biodiversity	817
		Pest and disease control (habitat for natural enemies)	114
Soil formation and composition (weathering, decomposition, mineralization)		307	
Climate regulation (gas and carbon sequestration, temperature stabilization)		103	
Cultural	<i>Physical and intellectual interactions with nature</i>	Experiential use of plants, animals and settings (bird watching, hiking)	4
		Physical use of plants, animals and settings (leisure hunting)	10
		Scientific, educational use of plants, animals and settings (subject matters)	7
	<i>Spiritual and symbolic interactions with nature</i>	Emblematic or sacred plants, animals or setting (sacred trees)	19
		Existence and bequest (enjoyment of wilderness, conservation for future generation)	0

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1354 **Box 1**

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1357 **Box 1 – Glossary**

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1359 **Ecological processes**

1360 Ecological processes are defined as the complex interactions between the biotic and abiotic elements of
1361 ecosystems that underpin fluxes of information (e.g., stimuli), energy (e.g., sunlight) and matter (e.g.,
1362 nutrients, gases, water) (Mace et al. 2012; Puydarieux and Beyou 2017). This concept is "organisms-
1363 centred"; the processes involved may be physiological (e.g. photosynthesis, respiration), biological (e.g.,
1364 dispersal) and/or evolutionary (e.g., selection or mutation).

1365 **Ecosystem functions**

1366 Ecosystem functions are the ecological (biological, chemical and physical) mechanisms that support the
1367 integrity or maintenance of ecosystems. This concept is "ecosystem-centred". Ecosystem functions, such
1368 as primary production or decomposition, result from interactions between ecosystem structures and
1369 processes (Ansink et al. 2008). They are not necessarily transformed into a benefit for humans. They are
1370 sometimes considered ecosystem "supporting services" (e.g., Millennium Ecosystem Assessment 2005).

1371 **Ecosystem services**

1372 Ecosystem services represent the contributions that ecosystems make to human well-being. Therefore,
1373 this concept is "human-centred". These services are defined according to their specific benefits to
1374 individuals or society. They are considered ecosystem services because they retain a connection to the
1375 underlying ecosystem functions that generate them. They are sometimes called final ecosystem services
1376 because they are outcomes from ecosystems that lead directly to goods that are valued for their
1377 contribution to human well-being (Mace et al. 2012; CICES 2013). They are typically subdivided into
1378 provisioning, regulation and cultural services.

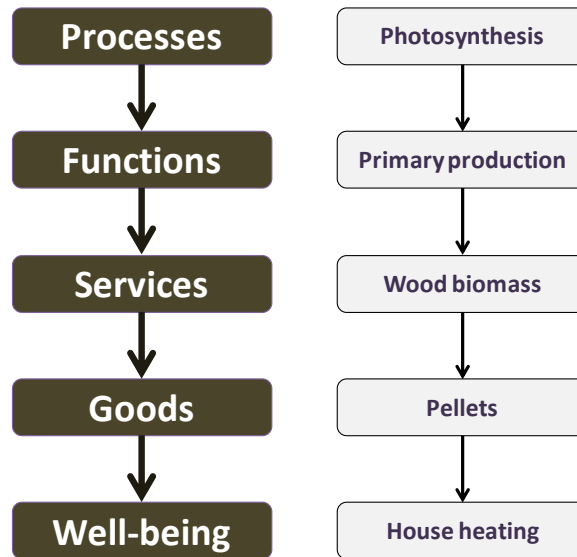
1379 **Ecosystem goods**

1380 Ecosystem goods are the products or benefits people can derive from final ecosystem services. Their value
1381 is not solely provided by ecosystems and may involve additional inputs from society, for example through
1382 human transformation or engineering. These goods may be material or immaterial, have value (monetary
1383 or otherwise) for people (Turner et al. 2000), and help to improve human well-being.

1384 **Human well-being**

1385 Human well-being includes the basic requirements for satisfactory living conditions, freedom and choice,
1386 health, good social relations, and security (Millennium Ecosystem Assessment 2005). Ecosystem goods
1387 may partly fulfill these requirements.

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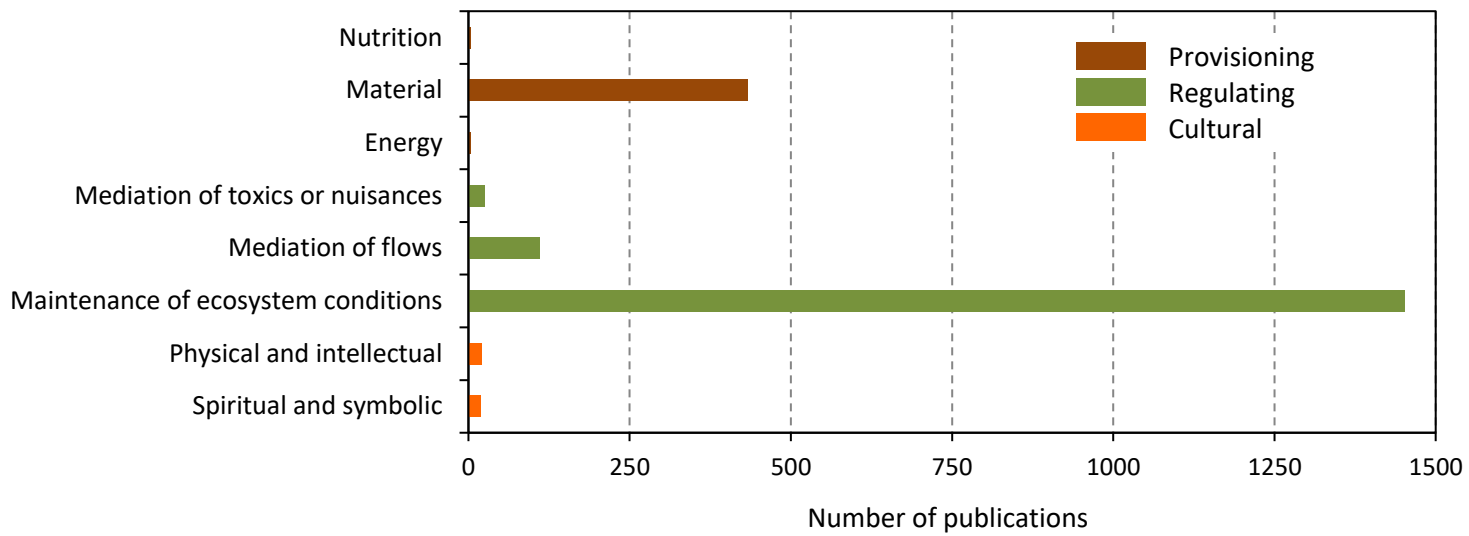


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Example of dependencies between human well-being and ecological processes via ecosystem functions, services, and goods or products.

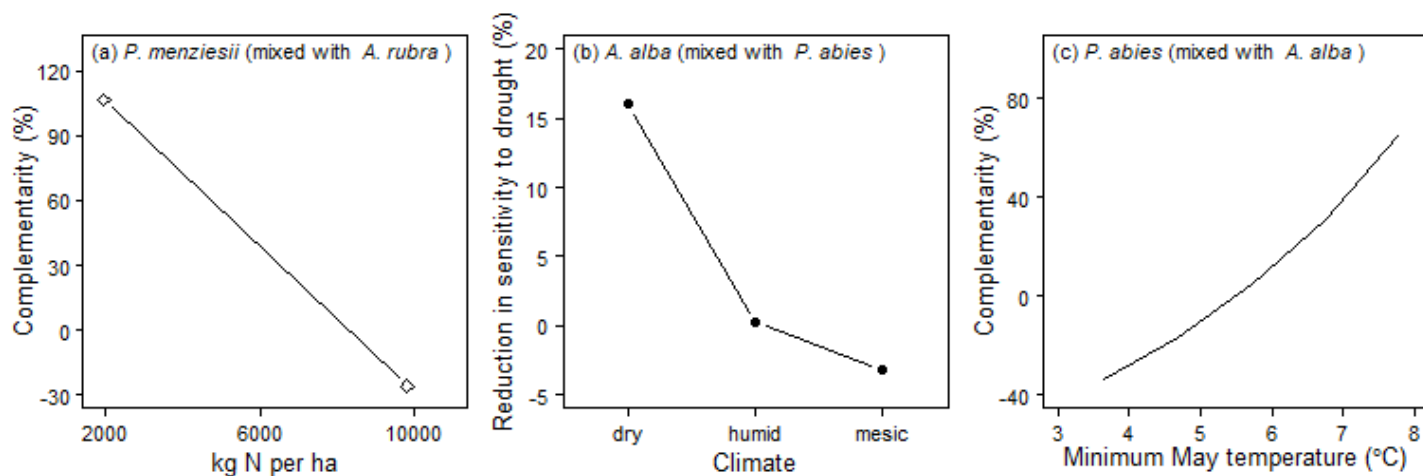
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1399 **Figures and captions**
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1401 **Figure 1.** Number of publications on provisioning, regulating and cultural ecosystem services referring to
1402 mixed-species forests according to a Web of Science keyword search of selected terms relating to
1403 ecosystem services (see Online Resource 1 for details).
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1408 **Figure 2.** Spatial changes in complementarity. Panel (a) shows declining complementarity for
1409 *Pseudotsuga menziesii* growing with the N-fixing *Alnus rubra* as soil N increased (Binkley 2003). Panel (b)
1410 shows how the relative reduction in drought sensitivity (%) of *Abies alba* (mixed with *Picea abies*) was
1411 lower on more moist sites (Lebourgeois et al. 2013). Panel (c) shows increasing complementarity effects
1412 for *P. abies* (mixed with *A. alba*) as growing conditions improved (quantified as mean minimum May
1413 temperature) (Forrester et al. 2013). Figure modified from Forrester (2014).
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