

## **Forest biodiversity, ecosystem functioning and the provision of ecosystem services**

Eckehard G. Brockerhoff, Luc Barbaro, Bastien Castagneyrol, David I. Forrester, Barry Gardiner, Jose Ramon González, Phil O'B. Lyver, Nicolas Meurisse, Anne Oxbrough, Hisatomo Taki, Ian D. Thompson, Fons van der Plas, Hervé Jactel

E. G. Brockerhoff (correspondence)

Scion (New Zealand Forest Research Institute), PO Box 29237, Christchurch 8440, New Zealand  
e-mail: [eckehard.brockerhoff@scionresearch.com](mailto:eckehard.brockerhoff@scionresearch.com)

L. Barbaro

Dynafor, INPT, El Purpan, INRA, Univ. Toulouse, Auzeville, France

B. Castagneyrol, H. Jactel

BIOGECO, INRA, University of Bordeaux, 33610 Cestas, France

D. I. Forrester

Swiss Federal Institute of Forest, Snow and Landscape Research WSL, 8903 Birmensdorf, Switzerland

B. Gardiner

EFI Atlantic, 69 Route d'Arcachon, 33612 Cestas, France

J. R. González

Forest Sciences Centre of Catalonia, CTFC, Ctra de St. Llorenç de Morunys, km 2, 25280 Solsona, Spain

P. O'B. Lyver

Manaaki Whenua - Landcare Research, PO Box 69040, Lincoln 7640, New Zealand

N. Meurisse

Scion (New Zealand Forest Research Institute), 49 Sala Street, Rotorua 3046, New Zealand

A. Oxbrough

Department of Biology, Edge Hill University, Ormskirk, Lancashire, L39 4QP, UK

H. Taki

Forestry and Forest Products Research Institute, 1 Matsunosato, Tsukuba, Ibaraki 305-8687, Japan

I. D. Thompson

Natural Resources Canada, Canadian Forest Service, Sault Ste. Marie, Ontario, Canada, P6A 2E5

F. van der Plas

Department of Systematic Botany and Functional Biodiversity, University of Leipzig, Johannisallee 21-23, 04103 Leipzig, Germany

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).

823

824

825 **References**

- 826
- 827 Aizen MA, Feinsinger P (1994) Forest fragmentation, pollination, and plant reproduction in a Chaco dry  
828 forest, Argentina. *Ecology* 75:330–351
- 829 Ansink E, Hein L, Hasund KP (2008) To value functions or services? An analysis of ecosystem valuation  
830 approaches. *Environ Values* 17:489–503
- 831 Anzures-Dadda A, Andresen E, Martínez ML et al (2011) Absence of howlers (*Alouatta palliata*)  
832 influences tree seedling densities in tropical rain forest fragments in southern Mexico. *Int J*  
833 *Primatol* 32:634–651
- 834 Aslam TJ, Benton TG, Nielsen UN, Johnson SN (2015) Impacts of eucalypt plantation management on soil  
835 faunal communities and nutrient bioavailability: trading function for dependence? *Biol Fertil Soils*  
836 51:637–644
- 837 Aspinwall MJ, King JS, McKeand SE, Bullock BP (2011) Genetic effects on stand-level uniformity and  
838 above- and belowground dry mass production in juvenile loblolly pine. *For Ecol Manage* 262:609–  
839 619
- 840 Balvanera P, Pfisterer AB, Buchmann N, et al. (2006). Quantifying the evidence for biodiversity effects on  
841 ecosystem functioning and services. *Ecol Lett* 9:1146–1156
- 842 Barbaro L, Brockerhoff EG, Giffard B, van Halder I (2012) Edge and area effects on avian assemblages  
843 and insectivory in fragmented native forests. *Landscape Ecol* 27:1451–1463
- 844 Barbosa P, Hines J, Kaplan I, Martinson H, Szczepaniec A, Szendrei Z (2009) Associational resistance and  
845 associational susceptibility: having right or wrong neighbors. *Annu Rev Ecol Evol Sys* 40:1–20
- 846 Barlow J, Gardner TA, Araujo IS, Perez CA, et al. (2007) Quantifying the biodiversity value of tropical  
847 primary, secondary, and plantation forests. *Proc Natl Acad Sci USA* 104:18555–18560
- 848 Barnes AD, Allen K, Kreft H, Haneda NF, et al (2017) Direct and cascading impacts of tropical land-use  
849 change on multi-trophic biodiversity. *Nature Ecol Evol*. doi:10.1038/s41559-017-0275-7
- 850 Barton KE, Valkama E, Vehviläinen H, Ruohomäki K, Knight TM, Koricheva J (2015) Additive and non-  
851 additive effects of birch genotypic diversity on arthropod herbivory in a long-term field experiment.  
852 *Oikos* 124:697–706
- 853 Bauhus J, van der Meer P, Kanninen M (eds) (2010) Ecosystem goods and services from plantation  
854 forests. Routledge, London
- 855 Beaune D, Fruth B, Bollache L et al (2013) Doom of the elephant-dependent trees in a Congo tropical  
856 forest. *For Ecol Manag* 295:109–117
- 857 Berndt L, Brockerhoff EG, Jactel H (2008) Relevance of exotic pine plantations as a surrogate habitat for  
858 ground beetles (Carabidae) where native forest is rare. *Biodivers Conserv* 9:247–261
- 859 Binkley D (2003) Seven decades of stand development in mixed and pure stands of conifers and  
860 nitrogen-fixing red alder. *Can J For Res* 33:2274–2279
- 861 Binkley D, Sollins P, Bell R, Sachs D, Myrold D (1992) Biogeochemistry of adjacent conifer and alder-  
862 conifer stands. *Ecology* 73:2022–2033
- 863 Binkley D, Stape JL, Bauerle WL, Ryan MG (2010) Explaining growth of individual trees: Light interception  
864 and efficiency of light use by *Eucalyptus* at four sites in Brazil. *For Ecol Manage* 259:1704–1713
- 865 Boafo YA, Saito O, Kato S, Kamiyama C, Takeuchi K, Nakahara M (2016) The role of traditional ecological  
866 knowledge in ecosystem services management: the case of four rural communities in Northern  
867 Ghana. *Int J Biodivers Sci Ecosyst Serv Manage* 12:24–38. doi:10.1080/21513732.2015.1124454

- 868 Bond WJ, Keeley JE (2005) Fire as a global 'herbivore': the ecology and evolution of flammable  
869 ecosystems. *Trends Ecol Evol* 20:387–394
- 870 Bond WJ, Midgley JJ (1995) Kill thy neighbour: an individualistic argument for the evolution of  
871 flammability. *Oikos* 73:79–85
- 872 Bonnesoeur V (2016) Acclimatation des arbres forestiers au vent : de la perception du vent à ses  
873 conséquences sur la croissance et le dimensionnement des tiges. AgroParisTech
- 874 Bourdier T, Cordonnier T, Kunstler G, Piedallu C, Lagarrigues G, Courbaud B (2016) Tree size inequality  
875 reduces forest productivity: An analysis combining inventory data for ten European species and a  
876 light competition model. *PLoS ONE* 11:e0151852.
- 877 Boyd IL, Freer-Smith PH, Gilligan CA, Godfray HC (2013) The consequence of tree pests and diseases for  
878 ecosystem services. *Science* 342:1235773. doi:10.1126/science.1235773
- 879 Brockerhoff EG, Jactel H, Parrotta JA, Ferraz SF (2013) Role of eucalypt and other planted forests in  
880 biodiversity conservation and the provision of biodiversity-related ecosystem services. *For Ecol*  
881 *Manage* 301:43–50
- 882 Brockerhoff EG, Jactel H, Parrotta JA, Quine CP, Sayer J (2008) Plantation forests and biodiversity:  
883 oxymoron or opportunity? *Biodivers Conserv* 17:925–951
- 884 Brockerhoff EG, Liebhold AM (2017) Ecology of forest insect invasions. *Biol Invas.* doi:10.1007/s10530-  
885 017-1514-1
- 886 Brockway DG, Gatewood RG, Paris RB (2002) Restoring fire as an ecological process in shortgrass prairie  
887 ecosystems: initial effects of prescribed burning during the dormant and growing seasons. *J*  
888 *Environ Manage* 65:135–152
- 889 Brodie JF, Aslan CE (2012) Halting regime shifts in floristically intact tropical forests deprived of their  
890 frugivores. *Restor Ecol* 20:153–157
- 891 Bueno RS, Guevara R, Ribeiro MC et al (2013) Functional redundancy and complementarities of seed  
892 dispersal by the last Neotropical megafugivores. *PLoS ONE* 8:e56252
- 893 Burgar JM, Craig MD, Stokes VL (2015) The importance of mature forest as bat roosting habitat within a  
894 production landscape. *For Ecol Manage* 356:112–123
- 895 Campos-Arceiz A, Blake S (2011) Megagardeners of the forest—the role of elephants in seed dispersal.  
896 *Acta Oecol* 37:542–553
- 897 Castagneyrol B, Jactel H (2012) Unraveling plant-animal diversity relationships: a meta-regression  
898 analysis. *Ecology* 93:2115–2124
- 899 Castagneyrol B, Jactel H, Vacher C, Brockerhoff EG, Koricheva J (2014a) Effects of plant phylogenetic  
900 diversity on herbivory depend on herbivore specialization. *J Appl Ecol* 51:134–141
- 901 Castagneyrol B, Régolini M, Jactel H (2014b) Tree species composition rather than diversity triggers  
902 associational resistance to the pine processionary moth. *Basic Appl Ecol* 15:516–523
- 903 Cavanaugh KC, Gosnell JS, Davis SL, Ahumada J, Boundja P, Clark DB, Mugerwa B, Jansen PA, O'Brien TG,  
904 Rovero F, Sheil D (2014) Carbon storage in tropical forests correlates with taxonomic diversity and  
905 functional dominance on a global scale. *Global Ecol Biogeog* 23:563–573
- 906 Chan KMA, Satterfield T, Goldstein J (2012) Rethinking ecosystem services to better address and  
907 navigate cultural values. *Ecol Econ* 74:8–18
- 908 Charbonnier Y, Gaüzère P, van Halder I, Nezan J, Barnagaud JY, Jactel H, Barbaro L (2016) Deciduous  
909 trees increase bat diversity at stand and landscape scales in mosaic pine plantations. *Landscape*  
910 *Ecol* 31:291–300

- 911 Chavez V, MacDonald E (2012) Partitioning vascular understory diversity in mixedwood boreal forests:  
912 The importance of mixed canopies for diversity conservation. *For Ecol Manage* 271:19–26
- 913 Chhatre A, Agrawal A (2009) Trade-offs and synergies between carbon storage and likelihood benefits  
914 from forest commons. *Proc Nat Acad Sci USA* 106(42):17667–17670.  
915 doi:10.1073/pnas.0905308106
- 916 CICES (2013) Common International Classification of Ecosystem Services (CICES): consultation on version  
917 4, August-December 2012. Centre for Environmental Management, Nottingham  
918 <http://cices.eu/content/uploads/sites/8/2015/09/CICES-V4-3--17-01-13a.xlsx>
- 919 Cockle KL, Martin K, Wesołowski T (2011) Woodpeckers, decay, and the future of cavity-nesting  
920 vertebrate communities worldwide. *Front Ecol Environ* 9:377–382
- 921 Conti G, Diaz S (2013) Plant functional diversity and carbon storage – an empirical test in semi-arid  
922 forest ecosystems. *J Ecol* 101:18–28
- 923 Cooper-Ellis S, Foster DR, Carlton G, Lezberg A (1999) Forest response to catastrophic wind: results from  
924 an experimental hurricane. *Ecology* 80:2683–2696
- 925 Coote L, Dietzsch AC, Wilson MW, Graham CT, Fuller L, Walsh AT, Irwin S, Kelly DL, Mitchell FJG, Kelly TC,  
926 O'Halloran J (2013) Testing indicators of biodiversity for plantation forests. *Ecol Indic* 32:107–115
- 927 Corona P, Franceschi S, Pisani C, Portoghesi L, Mattioli W, Fattorini L (2017) Inference on diversity from  
928 forest inventories: a review. *Biodivers Conserv*. doi:10.1007/s10531-015-1017-2
- 929 Cortes-Flores J, Andresen E, Cornejo-Tenorio G et al (2013) Fruiting phenology of seed dispersal  
930 syndromes in a Mexican neotropical temperate forest. *For Ecol Manag* 289:445–454
- 931 Costanza R, d'Arge R, De Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill RV, Paruelo  
932 J, Raskin RG (1997) The value of the world's ecosystem services and natural capital. *Nature*  
933 387:253-260
- 934 Côté S, Rooney T, Tremblay J (2004) Ecological impacts of deer overabundance. *Annu Rev Ecol Evol*  
935 *System* 35:113–147
- 936 Damien M, Jactel H, Meredieu C, Régolini M, van Halder I, Castagneyrol B. (2016) Pest damage in mixed  
937 forests: disentangling the effects of neighbour identity, host density and host apparency at different  
938 spatial scales. *Forest Ecol Manag* 378:103–110
- 939 Daniel TC, Muhar A, Arnberger A, Aznar O, Boyd JW, Chan KMA, Costanza R, Elmquist T, Flint CG,  
940 Gobster PH, Gret-Regamey A, Lave R, Muhar ., Penker M, Ribe RG, Schauppenlehner T, Sikor T,  
941 Soloviy I, Spierenburg M, Taczanowska K, Tam J, von der Dunk A (2012) Contributions of cultural  
942 services to the ecosystem services agenda. *Proc Nat Acad Sci USA* 109:8812–8819
- 943 de Vries FT, Thébault E, Liiri M, Bardgett RD, et al (2013) Soil food web properties explain ecosystem  
944 services across European land use systems. *Proc Nat Acad Sci* 110:14296–14301
- 945 Decocq G, Andrieu E, Brunet J, et al (2016) Ecosystem services from small forest patches in agricultural  
946 landscapes. *Curr For Rep* 2:30–44
- 947 Deconchat M, Brockerhoff EG, Barbaro L (2009) Effects of surrounding landscape composition on the  
948 conservation value of native and exotic habitats for native forest birds. *For Ecol Manage*  
949 258:S196–S204.
- 950 Dickinson MB, Johnson EA (2004) Temperature-dependent rate models of vascular cambium cell  
951 mortality. *Can J For Res* 34:546–559
- 952 Dupont S, Pivato D, Brunet Y (2015) Agricultural and Forest Meteorology Wind damage propagation in  
953 forests. *Agric For Meteorol* 214-215:243–251. doi:10.1016/j.agrformet.2015.07.010

- 954 Edwards D, Collins T, Goto R (2016) Does the conservation status of a Caledonian forest also indicate  
 955 cultural ecosystem value. In: Agnoletti M, Emanuelli F (eds) Biocultural diversity in Europe.  
 956 Springer International, New York
- 957 Everham III EM, Brokaw NVL (1996) Forest damage and recovery from catastrophic wind. *Bot Rev*  
 958 62:113–185
- 959 Fagerholm N, Käyhkö N, Ndumbaro F, Khamis M (2012) Community stakeholders' knowledge in  
 960 landscape assessments – mapping indicators for landscape services. *Ecol Indic* 18:421–433
- 961 Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Evol Syst* 34:487–515
- 962 Fahrig L et al (2015) Farmlands with smaller crop fields have higher within-field biodiversity. *Agric*  
 963 *Ecosyst Environ* 200:219–234
- 964 FAO (2015) Global Forest Resources Assessment 2015. FAO (Food and Agriculture Organization of the  
 965 United Nations), Rome
- 966 Farwig N, Sajita N, Bohning-Gaese K (2008) Conservation value of forest plantations for bird  
 967 communities in western Kenya. *For Ecol Manage* 255:3885–3892
- 968 Fernandes P, Luz A, Loureiro C (2010) Changes in wildfire severity from maritime pine woodland to  
 969 contiguous forest types in the mountain of northwestern Portugal. *For Ecol Manage* 260:883–892
- 970 Fernandez-Conradi P, Jactel H, Hampe A, Leiva MJ, Castagneyrol B (2017) The effect of tree genetic  
 971 diversity on insect herbivory varies with insect abundance. *Ecosphere* 8:e01637.  
 972 doi:10.1002/ecs2.1637
- 973 Finegan B, Peña-Claros M, Oliveira A, Ascarrunz N, Bret-Harte MS, Carreño-Rocabado G, Casanoves F,  
 974 Díaz S, Eguiguren Velepucha P, Fernandez F, Licona JC (2015) Does functional trait diversity  
 975 predict above-ground biomass and productivity of tropical forests? Testing three alternative  
 976 hypotheses. *J Ecol* 103:191–201
- 977 Forest Peoples Programme (2017) Forest Peoples Programme. Fosseyway Business Centre, Moreton-in-  
 978 Marsh. www.forestpeoples.org
- 979 Forrester DI (2014) The spatial and temporal dynamics of species interactions in mixed-species forests:  
 980 From pattern to process. *For Ecol Manage* 312:282–292
- 981 Forrester DI, Ammer C, Annighöfer PJ, Bravo-Oviedo A, et al (2017) Using the 3-PGmix model to predict  
 982 the spatial and temporal dynamics of species interactions in *Fagus sylvatica* and *Pinus sylvestris*  
 983 forests across Europe. *For Ecol Manage* 405:112–133
- 984 Forrester DI, Bauhus J (2016) A review of processes behind diversity - productivity relationships in  
 985 forests. *Curr For Rep* 2:45–61
- 986 Forrester DI, Kohnle U, Albrecht AT, Bauhus J (2013) Complementarity in mixed-species stands of *Abies*  
 987 *alba* and *Picea abies* varies with climate, site quality and stand density. *For Ecol Manage* 304:233–  
 988 242
- 989 Freer-Smith PH, Webber JF (2017) Tree pests and diseases: the threat to biodiversity and the delivery of  
 990 ecosystem services. *Biodiv Conserv*. doi:10.1007/s10531-015-1019-0
- 991 Fründ J, Dormann CF, Holzschuh A, Tschardt T (2013) Bee diversity effects on pollination depend on  
 992 functional complementarity and niche shifts. *Ecology* 94:2042–2054
- 993 Gamfeldt L, Snäll T, Bagchi R, Bengtsson J, et al. (2013) Higher levels of multiple ecosystem services are  
 994 found in forests with more tree species. *Nat Commun* 4:1340. doi:10.1038/ncomms2328
- 995 Garcia D, Martinez D (2012) Species richness matters for the quality of ecosystem services: a test using  
 996 seed dispersal by frugivorous birds. *Proc R Soc B* 279:3106–3113

- 997 Gardiner B, Marshall B, Achim A, Belcher R, Wood C (2005) The stability of different silvicultural systems:  
998 A wind-tunnel investigation. *Forestry* 78:471–484
- 999 Gardiner B, Schuck A, Schelhaas M-J, Orazio C, Blennow K, Nicoll B (2013) Living with Storm Damage to  
1000 Forests: What Science Can Tell Us. European Forest Institute, Joensuu.
- 1001 Garibaldi LA, Steffan-Dewenter I, Winfree R, Aizen MA, Bommarco R, Cunningham SA, Kremen C,  
1002 Carvalho LG, Harder LD, Afik O, Bartomeus I (2013) Wild pollinators enhance fruit set of crops  
1003 regardless of honey bee abundance. *Science* 339:1608–1611
- 1004 Gibson L, Lee TM, Koh LP, Sodhi NS, et al (2011) Primary forests are irreplaceable for sustaining tropical  
1005 biodiversity. *Nature* 478:378–381
- 1006 Gonzales RS, Ingle NR, Lagunzad DA, Nakashizuka T (2009) Seed dispersal by birds and bats in lowland  
1007 Philippine forest successional area. *Biotropica* 41:452–458
- 1008 González JR, Palahi M, Trasobares A, Pukkala T (2006) A fire probability model for forest stands in  
1009 Catalonia (north-east Spain). *Ann For Sci* 63:169–176
- 1010 González JR, Trasobares A, Palahi M, Pukkala T (2007) Predicting stand damage and tree survival in  
1011 burned forests in Catalonia (North-East Spain). *Ann For Sci* 64:733–742
- 1012 Gonzalez P, Kroll B, Vargas CR (2014) Tropical rainforest biodiversity and aboveground carbon changes  
1013 and uncertainties in the Selva Central, Peru. *For Ecol Manage* 312:78–91
- 1014 Gonzalez-Varo JP, Lopez-Bao JV, Guitian J (2013) Functional diversity among seed dispersal kernels  
1015 generated by carnivorous mammals. *J Anim Ecol* 82:562–571
- 1016 Gould RK, Ardoin NM, Woodside U, Satterfield T, Hannahs N, Daily GC (2014) The forest has a story:  
1017 cultural ecosystem services in Kona, Hawai'i. *Ecol Soc* 19:55. doi:10.5751/ES-06893-190355
- 1018 Graham CT, Wilson MW, Gittings T, Kelly TC, Irwin S, Quinn JL, O'Halloran J (2017) Implications of  
1019 afforestation for bird communities: the importance of preceding land-use type. *Biodiv Conserv*.  
1020 doi:10.1007/s10531-015-0987-4
- 1021 Gregory RD, Vorisek P, van Strien A, Gmelig Meyling AW, Jiguet F, Fornasari L, Reif J, Chylarecki P,  
1022 Burfield IJ (2007) Population trends of widespread woodland birds in Europe. *Ibis* 149:78–97
- 1023 Guyot V, Castagneyrol B, Vialatte A, Deconchat M, Jactel H (2016) Tree diversity reduces pest damage in  
1024 mature forests across Europe. *Biol Lett* 12: 20151037
- 1025 Guyot V, Castagneyrol B, Vialatte A, Deconchat M, Selvi F, Bussotti F, Jactel H (2015) Tree diversity limits  
1026 the impact of an invasive forest pest. *PloS ONE* 10: e0136469
- 1027 Hambäck PA, Englund G (2005) Patch area, population density and the scaling of migration rates: the  
1028 resource concentration hypothesis revisited. *Ecol Lett* 8: 1057–1065
- 1029 Hanewinkel M, Albrecht A, Schmidt M (2013) Influence of stand characteristics and landscape structure  
1030 on wind damage. In: Gardiner B, Schuck A, Schelhaas M, Orazio C, Blennow K, Nicoll B (eds), *Living*  
1031 *with Storm Damage to Forests: What Science Can Tell Us*. European Forest Institute, pp 41–47
- 1032 Harmon ME, Fath B, Woodall CW, Sexton J (2013) Carbon concentration of standing and downed  
1033 woody detritus: Effects of tree taxa, decay class, position, and tissue type. *For Ecol Manage*  
1034 291:259–267
- 1035 Häyhä T, Franzese PP, Alessandro Paletto A, Fath BD (2015) Assessing, valuing, and mapping ecosystem  
1036 services in alpine forests. *Ecosyst Serv* 14:12–23.
- 1037 Hector A, Bagchi R (2007) Biodiversity and ecosystem multifunctionality. *Nature* 448:188–190.  
1038 doi:10.1038/nature05947

- 1039 Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem  
1040 S, Schmid B (2005). Effects of biodiversity on ecosystem functioning: a consensus of current  
1041 knowledge. *Ecol Monogr* 75:3–35
- 1042 Irwin S, Pedley S, Coote L, Dietzsch A, Wilson M, Oxbrough A, Sweeney O, Moore K, Martin R, Kelly D,  
1043 Mitchell FG, Kelly T, O’Halloran J (2014) The value of plantation forests for plant, invertebrate and  
1044 bird diversity and the potential for cross-taxon surrogacy. *Biodivers Conserv* 23:697–714
- 1045 Isbell F, Calcagno V, Hector A, et al (2011) High plant diversity is needed to maintain ecosystem services.  
1046 *Nature* 477:199–202
- 1047 Isbell F, Craven D, Connolly J, Loreau M, Eisenhauer N, et al (2015) Biodiversity increases the resistance  
1048 of ecosystem productivity to climate extremes. *Nature* 526:574–577
- 1049 Jactel H, Bauhus J, Boberg J, Bonal D, Castagneyrol B, Gardiner B, Gonzalez-Olabarria JR, Koricheva J,  
1050 Meurisse N, Brockerhoff EG (2017) Tree diversity drives forest stand resistance to natural  
1051 disturbances. *Curr For Rep* 3:223–243
- 1052 Jactel H, Birgersson G, Andersson S, Schlyter F (2011) Non-host volatiles mediate associational resistance  
1053 to the pine processionary moth. *Oecologia* 166:703–711
- 1054 Jactel H, Brockerhoff EG (2007) Tree diversity reduces herbivory by forest insects. *Ecol Lett* 10:835–848
- 1055 Jactel H, Brockerhoff E, Duelli P (2005) A test of the biodiversity-stability theory: Meta-analysis of tree  
1056 species diversity effects on insect pest infestations, and re-examination of responsible factors. In:  
1057 Scherer-Lorenzen M, Körner C, Schulze ED (eds) *Forest Diversity and Function: Temperate and*  
1058 *Boreal Systems*. Springer, New York, pp235–262
- 1059 Jactel H, Menassieu P, Vetillard F, Gaulier A, Samalens JC, Brockerhoff EG (2006) Tree species diversity  
1060 reduces the invasibility of maritime pine stands by the bark scale, *Matsucoccus feytaudi*  
1061 (Homoptera: Margarodidae). *Can J For Res* 36:314–323
- 1062 Jesus FM, Pivello VR, Meirelles ST et al (2012) The importance of landscape structure forest seed  
1063 dispersal in rain forest fragments. *J Veg Sci* 23:1126–1136
- 1064 Jönsson MT, Ruete A, Kellner O, Gunnarsson U, Snäll T (2017) Will forest conservation areas protect  
1065 functionally important diversity of fungi and lichens over time? *Biodivers Conserv* 26:2547–2567
- 1066 Jung K, Kaiser S, Böhm S, Nieschulze J, Kalko EKV (2012) Moving in three dimensions: effects of  
1067 structural complexity on occurrence and activity of insectivorous bats in managed forest stands. *J*  
1068 *Appl Ecol* 49:523–531
- 1069 Keenan RJ, Reams GA, Achard F, et al (2015) Dynamics of global forest area: Results from the FAO Global  
1070 Forest Resources Assessment 2015. *For Ecol Manage* 352:9–20
- 1071 Kelty MJ (1992) Comparative productivity of monocultures and mixed-species stands. In: Kelty MJ,  
1072 Larson BC, Oliver CD (eds) *The Ecology and Silviculture of Mixed-Species Forests*. Kluwer Academic  
1073 Publishers, Dordrecht, pp 125–141
- 1074 Kennedy CM et al (2013) A global quantitative synthesis of local and landscape effects on wild bee  
1075 pollinators in agroecosystems. *Ecol Lett* 16:584–599
- 1076 Kirby KR, Potvin C (2007) Variation in carbon storage among tree species: Implications for the  
1077 management of a small-scale carbon sink project. *For Ecol Manage* 246:208–221
- 1078 Klein AM, Vaissiere BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007)  
1079 Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal*  
1080 *Society of London B* 274:303–313
- 1081 Kozlov MV, Lanta V, Zverev V, Zvereva EL (2015) Background losses of woody plant foliage to insects show  
1082 variable relationships with plant functional traits across the globe. *J Ecol* 103:1519–1528

- 1083 Kurz WA, Dymond CC, Stinson G, Rampley GJ, Neilson ET, Carroll AL, Ebata T, Safranyik L (2008) Mountain  
1084 pine beetle and forest carbon feedback to climate change. *Nature* 452:987–990
- 1085 Lange M, Eisenhauer N, Sierra CA, Bessler H, Engels C, Griffiths RI, Mellado-Vázquez PG, Malik AA, Roy J,  
1086 Scheu S, Steinbeiss S, Thomson BC, Trumbore SE, Gleixner G (2015) Plant diversity increases soil  
1087 microbial activity and soil carbon storage. *Nature Comm* 6:6707. doi:10.1038/ncomms7707
- 1088 Lebourgeois F, Gomez N, Pinto P, Mérian P (2013) Mixed stands reduce *Abies alba* tree-ring sensitivity to  
1089 summer drought in the Vosges mountains, western Europe. *For Ecol Manage* 303:61–71
- 1090 Lefcheck JS, Byrnes JE, Isbell F, Gamfeldt L, Griffin JN, Eisenhauer N, Hensel MJ, Hector A, Cardinale BJ,  
1091 Duffy JE (2015) Biodiversity enhances ecosystem multifunctionality across trophic levels and  
1092 habitats. *Nature Comm* 6: 6936. doi:10.1038/ncomms7936
- 1093 Lehouck V, Spanhove T, Colson L et al (2009) Habitat disturbance reduces seed dispersal of a forest  
1094 interior tree in a fragmented African cloud forest. *Oikos* 118:1023–1034
- 1095 Liang J, Crowther TW, Picard N, Wiser S, Reich PB, et al (2016) Positive biodiversity-productivity  
1096 relationship predominant in global forests. *Science* 354:aaf8957. doi:10.1126/science.aaf8957
- 1097 Liebhold AM, McCullough DG, Blackburn LM, Frankel SJ, Von Holle B, Aukema JE (2013) A highly  
1098 aggregated geographical distribution of forest pest invasions in the USA. *Divers Distrib* 19:1208–  
1099 1216
- 1100 Lindenmayer D, Blanchard W, Tennant P, Barton P, Ikin K, Mortelliti A, Okada S, Crane M, Michael D  
1101 (2015) Richness is not all: how changes in avian functional diversity reflect major landscape  
1102 modification caused by pine plantations. *Divers Distrib* 21:836–847
- 1103 Lindenmayer DB (2009) Forest wildlife management and conservation. *Ann NY Acad Sci* 1162:284–310
- 1104 Lindenmayer DB (2017) Conserving large old trees as small natural features. *Biol Cons* 211:51–59
- 1105 Lindenmayer DB, Franklin JF (2002) Conserving forest biodiversity: a comprehensive multiscaled  
1106 approach. Island Press, Washington
- 1107 Linnell MA, Davis RJ, Lesmeister DB, Swingle JK (2017) Conservation and relative habitat suitability for an  
1108 arboreal mammal associated with old forest. *For Ecol Manage* 402:1–11
- 1109 Lovelock CE, Ewel JJ (2005) Links between tree species, symbiotic fungal diversity and ecosystem  
1110 functioning in simplified tropical ecosystems. *New Phytol* 167:219–228
- 1111 Lutz DA, Burakowski EA, Murphy MB, Borsuk ME, Niemiec RM, Howarth RB (2016) Trade-offs between  
1112 three forest ecosystem services across the state of New Hampshire, USA: timber, carbon, and  
1113 albedo. *Ecol Appl* 26:146–161. doi:10.1890/14-2207
- 1114 Luu TC, Binkley D, Stape JL (2013) Neighborhood uniformity increases growth of individual *Eucalyptus*  
1115 trees. *For Ecol Manage* 289:90–97
- 1116 Lyver PO'B, Timoti P, Gormley A, Jones CJ, Richardson SJ, Tahī BL, Greenhalgh S (2017) Key Māori values  
1117 strengthen the mapping of forest ecosystem services. *Ecosyst Serv* 27:92–102
- 1118 Lyver PO'B, Timoti P, Jones CJ, Richardson SJ, Tahī BL, Greenhalgh S (2017) An indigenous community-  
1119 based monitoring system for assessing forest health in New Zealand. *Biodiv Conserv.*  
1120 doi:10.1007/s10531-016-1142-6
- 1121 Mace G, Masundire H, Baillie J, et al. (2005) Biodiversity. In: Hassan R, Scholes R, Ash N (eds) *Ecosystems*  
1122 *and human well-being: Current state and trends: Findings of the Condition and Trends Working*  
1123 *Group (Chapter 4); Millennium Ecosystem Assessment.* Island Press, Washington
- 1124 Mace GM, Norris K, Fitter AH (2012) Biodiversity and ecosystem services: a multilayered relationship.  
1125 *Trends Ecol Evol* 27:19–26. doi:10.1016/j.tree.2011.08.006



- 1126 Markl JS, Schleuning M, Forestget PM et al (2012) Meta-analysis of the effects of human disturbance on  
1127 seed dispersal by animals. *Conserv Biol* 26:1072–1081
- 1128 Martín-Alcón S, Coll L, De Cáceres M, Guitart L, Cabré M, Just A, González-Olabarría JR (2015) Combining  
1129 aerial LiDAR and multispectral imagery to assess postfire regeneration types in a Mediterranean  
1130 forest. *Can J For Res* 45:856–866
- 1131 Michener CD (2007) *The bees of the world* (2<sup>nd</sup> ed). The Johns Hopkins University Press, Baltimore
- 1132 Milcu AI, Hanspach J, Abson D, Fischer J (2013) Cultural ecosystem services: a literature review and  
1133 prospects for future research. *Ecol Soc* 18:44. doi:10.5751/ES-05790-180344
- 1134 Millennium Ecosystem Assessment (MEA) (2005) *Ecosystems and human well-being*. Island Press,  
1135 Washington
- 1136 Mitchell MGE, Bennett EM, Gonzalez A (2014) Forest fragments modulate the provision of multiple  
1137 ecosystem services. *J Appl Ecol* 51:909–918. doi:10.1111/1365-2664.12241
- 1138 Monge JJ, Parker WJ, Richardson JW (2016) Integrating forest ecosystem services into the farming  
1139 landscape: A stochastic economic assessment. *J Environ Manage* 174:87–99
- 1140 Moreira X, Abdala-Roberts L, Parra-Tabla V, Mooney KA (2014) Positive effects of plant genotypic and  
1141 species diversity on anti-herbivore defenses in a tropical tree species. *PLoS ONE* 9:e105438
- 1142 Mori AS, Isbell F, Fujii S, Makoto K, Matsuoka S, Osono T (2016) Low multifunctional redundancy of soil  
1143 fungal diversity at multiple scales. *Ecol Lett* 19:249–259. doi:10.1007/s11284-016-1367-6
- 1144 Mori AS, Lertzman KP, Gustafsson L (2017) Biodiversity and ecosystem services in forest ecosystems: a  
1145 research agenda for applied forest ecology. *J Appl Ecol* 54:12–27
- 1146 Muiruri EW, Rainio K, Koricheva J (2016) Do birds see the forest for the trees? Scale-dependent effects of  
1147 tree diversity on avian predation of artificial larvae. *Oecologia* 180:619–630
- 1148 Neumann JL, Holloway GJ, Hoodless A, Griffiths GH (2017) The legacy of 20th Century landscape change  
1149 on today's woodland carabid communities. *Divers Distrib* doi:10.1111/ddi.12652
- 1150 Newbold T, Hudson LN, Hill SLL, et al (2015) Global effects of land use on local terrestrial biodiversity.  
1151 *Nature* 520:45–50
- 1152 Nikula A, Heikkinen S, Helle E (2004) Habitat selection of adult moose *Alces alces* at two spatial scales in  
1153 central Finland. *Wildlife Biol* 10:121–135
- 1154 O'Callaghan CJ, Irwin S, Byrne KA, O'Halloran J (2017) The role of planted forests in the provision of  
1155 habitat: an Irish perspective. *Biodivers Conserv*. doi:10.1007/s10531-016-1125-7
- 1156 Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? *Oikos*  
1157 120:321–326
- 1158 Osuri AM, Kumar VS, Sankaran M (2014) Altered stand structure and tree allometry reduce carbon  
1159 storage in evergreen forest fragments in India's Western Ghats. *For Ecol Manage* 329:375–383
- 1160 Oxbrough A, García-Tejero S, Spence J, O'Halloran J (2016) Can mixed stands of native and non-native tree  
1161 species enhance diversity of epigeic arthropods in plantation forests? *For Ecol Manage* 367:21-29
- 1162 Oxbrough A, Gittings T, O'Halloran J, Giller P, Kelly TC (2007) Biodiversity of the ground-dwelling spider  
1163 fauna of afforestation habitats. *Agric Ecosyst Environ* 120:433–441
- 1164 Pachauri RK, Allen MR, Barros VR, et al (2014) *Climate change 2014: synthesis report. Contribution of*  
1165 *Working Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on*  
1166 *Climate Change*. IPCC, Geneva
- 1167 Paquette A, Messier C (2010) The role of plantations in managing the world's forests in the  
1168 Anthropocene. *Frontiers Ecol Environ* 8:27–34

- 1169 Payn T, Carnus JM, Freer-Smith P, Kimberley M, Kollert W, Liu S, Orazio C, Rodriguez L, Silva LN,  
1170 Wingfield MJ (2015) Changes in planted forests and future global implications. *For Ecol Manage*  
1171 352:57–67. doi:10.1016/j.foreco.2015.06.021
- 1172 Penaluna BE, Olson DH, Flitcroft RL, Weber MA, Bellmore JR, Wondzell SM, Dunham JB, Johnson SL,  
1173 Reeves GH (2017) Aquatic biodiversity in forests: a weak link in ecosystem services resilience.  
1174 *Biodiv Conserv*. doi:10.1007/s10531-016-1148-0
- 1175 Pert PL, Hill R, Maclean K, Dale A, Rist P, Schmider J, Talbot L, Tawake L (2015) Mapping cultural  
1176 ecosystem services with rainforest aboriginal peoples: Integrating biocultural diversity,  
1177 governance and social variation. *Ecosyst Serv* 13:41–56
- 1178 Phifer CC, Knowlton JL, Webster CR, Flaspohler DJ, Licata JA (2017) Bird community responses to  
1179 afforested eucalyptus plantations in the Argentine pampas. *Biodivers Conserv*.  
1180 doi:10.1007/s10531-016-1126-6
- 1181 Plath M, Dorn S, Barrios H, Mody K (2012) Diversity and composition of arboreal beetle assemblages in  
1182 tropical pasture afforestations: effects of planting schemes and tree species identity. *Biodivers*  
1183 *Conserv* 21: 3423–3444
- 1184 Plieninger T, Sebastian Dijks S, Oteros-Rozas E, Bieling C (2013) Assessing, mapping and quantifying  
1185 cultural ecosystem services at community level. *Land Use Pol* 33:118–129
- 1186 Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator  
1187 declines: trends, impacts and drivers. *Trends Ecol Evolut* 25:345–353
- 1188 Potts SG, Imperatriz-Fonseca VL, Ngo HT, Biesmeijer JC, Breeze TD, Dicks LV, Garibaldi LA, Hill R, Settele  
1189 J, Vanbergen AJ (2016) Summary for policymakers of the assessment report of the  
1190 Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators,  
1191 pollination and food production. [https://www.actu-environnement.com/media/pdf/news-26331-](https://www.actu-environnement.com/media/pdf/news-26331-synthese-ipbes-decideurs-pollinisateurs.pdf)  
1192 [synthese-ipbes-decideurs-pollinisateurs.pdf](https://www.actu-environnement.com/media/pdf/news-26331-synthese-ipbes-decideurs-pollinisateurs.pdf)
- 1193 Pretzsch H, Forrester DI (2017) Stand dynamics of mixed-species stands compared with monocultures.  
1194 In: Pretzsch H, Forrester DI, Bauhus J (eds) *Mixed-Species Forests - Ecology and Management*.  
1195 Springer, Berlin, Heidelberg, pp 117–209
- 1196 Pretzsch H, Forrester DI, Bauhus J (eds) (2017) *Mixed-Species Forests - Ecology and Management*.  
1197 Springer, Berlin, Heidelberg.
- 1198 Proctor M, Yeo P, Lack A (1996) *The natural history of pollination*. HarperCollins, New York
- 1199 Puydarieux P, Beyou W (2017) Evaluation française des écosystèmes et des services écosystémique –  
1200 cadre conceptuel. Ministère de l'Environnement & Fondation pour la Recherche sur la  
1201 Biodiversité. [https://www.ecologique-solidaire.gouv.fr/sites/default/files/Thema%20-](https://www.ecologique-solidaire.gouv.fr/sites/default/files/Thema%20-%20Efese%20-%20Le%20cadre%20conceptuel.pdf)  
1202 [%20Efese%20-%20Le%20cadre%20conceptuel.pdf](https://www.ecologique-solidaire.gouv.fr/sites/default/files/Thema%20-%20Efese%20-%20Le%20cadre%20conceptuel.pdf)
- 1203 Quine CP, Malcolm DC (2007) Wind-driven gap development in Birkley Wood, a long-term retention of  
1204 planted Sitka spruce in upland Britain. *Can J For Res* 37:1787–1796. doi:10.1139/X07-051
- 1205 Ratcliffe S, Wirth C, Jucker T, Baeten L, et al (2017 in press) Biodiversity and ecosystem functioning  
1206 relations in European forests depend on environmental context. *Ecol Lett*. doi:10.1111/ele.12849
- 1207 Ribe RG (2005) Aesthetic perceptions of green tree retention harvests in vista views. The interaction of  
1208 cut level, retention pattern and harvest shape. *Landsc Urban Plan* 73:277–293
- 1209 Richards AE, Forrester DI, Bauhus J, Scherer-Lorenzen M (2010) The influence of mixed tree plantations  
1210 on the nutrition of individual species: a review. *Tree Physiology* 30:1192–1208
- 1211 Rickenbach O, Reyes-Gracia V, Moser G, Garcia C (2017) What explains wildlife value orientations? A  
1212 study among Central African forest dwellers. *Hum Ecol* 45:293–306

- 1213 Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of  
1214 collards (*Brassica oleracea*). *Ecol Monogr* 43:95–124
- 1215 Rubene D, Schroeder M, Ranius T (2015) Diversity patterns of wild bees and wasps in managed boreal  
1216 forests: effects of spatial structure, local habitat and surrounding landscape. *Biol Conserv*  
1217 184:201–208
- 1218 Ruffell J, Clout MN, Didham RK (2017) The matrix matters, but how should we manage it? Estimating the  
1219 amount of high-quality matrix required to maintain biodiversity in fragmented landscapes.  
1220 *Ecography* 40:171–178
- 1221 Ryan MG, Stape JL, Binkley D, Silva GGC, et al. (2010) Factors controlling *Eucalyptus* productivity: How  
1222 water availability and stand structure alter production and carbon allocation. *For Ecol Manage*  
1223 259:1695–1703
- 1224 Sangha KK, Russell-Smith J (2017) Towards an indigenous ecosystems services valuation framework: a  
1225 north Australian example. *Conserv Soc* 15:255–269
- 1226 Santaniello F, Djupström LB, Ranius T, Weslien J, Rudolphi J, Thor G (2017) Large proportion of wood  
1227 dependent lichens in boreal pine forest are confined to old hard wood. *Biodivers Conserv* 26:1295–  
1228 1310
- 1229 Schröter D, Cramer W, Leemans R, Zierl B, et al. (2005) Ecosystem service supply and vulnerability to  
1230 global change in Europe. *Science* 310:1333–1337
- 1231 Schuldt A, Baruffol M, Böhnke M, et al (2010) Tree diversity promotes insect herbivory in subtropical  
1232 forests of south-east China. *J Ecol* 98:917–926
- 1233 Schulze ED, Mooney HA (eds) (2012) *Biodiversity and ecosystem function*. Springer Science & Business  
1234 Media, Heidelberg
- 1235 Seibold S, Bassler C, Brandl R, Gossner MM, Thom S, Ulyshen MD, Muller J (2015) Experimental studies of  
1236 dead-wood biodiversity – A review identifying global gaps in knowledge. *Biol Conserv* 191:139–149
- 1237 Seidler TG, Plotkin JB (2006) Seed dispersal and spatial pattern in tropical trees. *PLoS Biol* 4:e344. doi:10.  
1238 1371/journal.pbio.0040344
- 1239 Shirima DD, Totland Ø, Munishi PK, Moe SR (2015) Relationships between tree species richness,  
1240 evenness and aboveground carbon storage in montane forests and miombo woodlands of  
1241 Tanzania. *Basic Appl Ecol* 16:239–249
- 1242 Sholes OD (2008) Effects of associational resistance and host density on woodland insect herbivores. *J*  
1243 *Anim Ecol* 77:16–23
- 1244 Smith GF, Gittings T, Wilson M, French L, Oxbrough A, O'Donoghue S, O'Halloran J, Kelly DL, Mitchell FJG,  
1245 Kelly T, Iremonger S, McKee A-M, Giller P (2008) Identifying practical indicators of biodiversity for  
1246 stand-level management of plantation forests. *Biodivers Conserv* 17:991–1015
- 1247 Soares AAV, Leite HG, Souza AL, Silva SR, Lourenço HM, Forrester DI (2016) Increasing stand structural  
1248 heterogeneity reduces productivity in Brazilian *Eucalyptus* monoclonal stands. *For Ecol Manage*  
1249 373:26–32
- 1250 Staab M, Schuldt A, Assmann T, Klein A (2014) Tree diversity promotes predator but not omnivore ants in  
1251 a subtropical Chinese forest. *Ecol Entomol* 39:637–647
- 1252 Stanturf JA, Goodrick SL, Outcalt KW (2007) Disturbance and coastal forests: A strategic approach to  
1253 forest management in hurricane impact zones. *For Ecol Manage* 250:119–135.  
1254 doi:10.1016/j.foreco.2007.03.015
- 1255 Stape JL, Binkley D, Ryan MG, Azevedo MR, et al. (2010) The Brazil *Eucalyptus* Potential Productivity  
1256 Project: Influence of water, nutrients and stand uniformity on wood production. *For Ecol Manage*  
1257 259:1684–1694

- 1258 Sturtevant BR, Miranda BR, Yang J, He HS, Gustafson EJ, Scheller RM (2009) Studying fire mitigation  
1259 strategies in multi-ownership landscapes: Balancing the management of fire-dependent  
1260 ecosystems and fire risk. *Ecosystems* 12:445–461
- 1261 Styring AR, Ragai R, Unggang J, Stuebing R, Hosner PA, Sheldon FH (2011) Bird community assembly in  
1262 Bornean industrial tree plantations: effects of forest age and structure. *For Ecol Manage* 261:531–  
1263 544
- 1264 Taki H, Ikeda H, Nagamitsu T, Yasuda M, Sugiura S, Maeto K, Okabe K (2017). Stable nitrogen and carbon  
1265 isotope ratios in wild native honeybees: the influence of land use and climate. *Biodiv Conserv*.  
1266 doi:10.1007/s10531-016-1114-x
- 1267 Taki H, Inoue T, Tanaka H, Makihara H, Sueyoshi M, Isono M, Okabe K (2010) Responses of community  
1268 structure, diversity, and abundance of understory plants and insect assemblages to thinning in  
1269 plantations. *For Ecol Manage* 259:607–613
- 1270 Taki H, Okochi I, Okabe K, Inoue T, Goto H, Matsumura T, Makino Si (2013) Succession influences wild  
1271 bees in a temperate forest landscape: The value of early successional stages in naturally  
1272 regenerated and planted forests. *PLoS ONE* 8:e56678
- 1273 Taki H, Yamaura Y, Okabe K, Maeto K (2011) Plantation vs. natural forest: Matrix quality determines  
1274 pollinator abundance in crop fields. *Sci Rep* 1:132. doi:10.1038/srep00132
- 1275 Terborgh J, Nunez-Iturii G, Pitman NCA, Cornejo-Valverde FH, Alvarez P, Swamy V, Pringle EG, Paine CET  
1276 (2008) Tree recruitment in an empty forest. *Ecology* 89:1757–1768
- 1277 Thom D, Seidl R (2016) Natural disturbance impacts on ecosystem services and biodiversity in temperate  
1278 and boreal forests. *Biol Rev* 91:760–781. doi:10.1111/brv.12193
- 1279 Thompson ID, Okabe K, Parrotta JA, Brockerhoff E, Jactel H, Forrester DI, Taki H (2014) Biodiversity and  
1280 ecosystem services: lessons from nature to improve management of planted forests for REDD-  
1281 plus. *Biodiv Conserv* 23:2613–35
- 1282 Thompson ID, Okabe K, Tylianakis JM, et al (2011). Forest biodiversity and the delivery of ecosystem  
1283 goods and services: translating science into policy. *Bio Science* 61:972–981
- 1284 Traveset A (1998) Effect of seed passage through vertebrate frugivores' guts on germination: a review.  
1285 *Perspect Plant Ecol Evol Syst* 1:151–190
- 1286 Turner RK, Van Den Bergh JC, Söderqvist T, Barendregt A, Van Der Straaten J, Maltby E, Van Ierland EC  
1287 (2000) Ecological-economic analysis of wetlands: scientific integration for management and  
1288 policy. *Ecol Econ* 35:7–23
- 1289 Tylianakis JM, Rand TA, Kahmen A, Klein A-M, Buchmann N, Perner J, Tschardt T (2008) Resource  
1290 heterogeneity moderates the biodiversity-function relationship in real world ecosystems. *PLoS*  
1291 *Biol* 6:e122
- 1292 Ulanova NG (2000) The effects of windthrow on forests at different spatial scales: a review. *For Ecol*  
1293 *Manage* 135:155–167
- 1294 Ulyshen MD (2016) Wood decomposition as influenced by invertebrates. *Biol Rev* 91:70–85
- 1295 Unsicker SB, Oswald A, Köhler G, Weisser WW (2008) Complementarity effects through dietary mixing  
1296 enhance the performance of a generalist insect herbivore. *Oecologia* 156:313–324
- 1297 van der Plas F, Ratcliffe S, Ruiz-Benito P, Allan E, et al. (2017) Continental mapping of forest ecosystem  
1298 functions reveals a high but unrealized potential for forest multifunctionality. *Ecol Lett*.  
1299 doi:10.1111/ele.12868
- 1300 van der Plas F, Manning P, Allan E, Fischer M, et al. (2016a) Jack-of-all-trades effects drive biodiversity-  
1301 ecosystem multifunctionality relationships in European forests. *Nat Commun* 7:11109.  
1302 doi:10.1038/ncomms11109

- 1303 van der Plas F, Manning P, Soliveres S, Fischer M, et al. (2016b) Biotic homogenisation can decrease  
 1304 landscape scale ecosystem multifunctionality. *Proc Nat Acad Sci USA* 113:357–362.  
 1305 doi:10.1073/pnas.1517903113
- 1306 Vangansbeke P, Blondeel H, Landuyt D, De Frenne P, Gorissen L, Verheyen K (2017) Spatially combining  
 1307 wood production and recreation with biodiversity conservation. *Biodiv Conserv.*  
 1308 doi:10.1007/s10531-016-1135-5
- 1309 Veres A, Petit S, Conord C, Lavigne C (2013) Does landscape composition affect pest abundance and their  
 1310 control by natural enemies? A review. *Agr Ecosyst Environ* 166:110–117
- 1311 Verkerk PJ, Mavsar R, Giergiczny M, Linder M, Edwards D, Schelhaas MJ (2014) Assessing impacts of  
 1312 increased biomass production and biodiversity protection on ecosystem services provided by  
 1313 European forests. *Ecosystem Services* 9:155–165. doi:10.1016/j.ecoser.2014.06.004
- 1314 Verschut TA, Becher PG, Anderson P, Hambäck PA (2016) Disentangling associational effects: both  
 1315 resource density and resource frequency affect search behaviour in complex environments. *Funct*  
 1316 *Ecol* 30:1826–1833
- 1317 Vilà M, Hulme PE (eds) (2016) Impact of biological invasions on ecosystem services. Springer  
 1318 International, Cham
- 1319 Wardle DA (2001) Experimental demonstration that plant diversity reduces invasibility—evidence of a  
 1320 biological mechanism or a consequence of sampling effect? *Oikos* 95:161–70
- 1321 Wear DN, Greis JG (2002) The southern forest resource assessment: summary report. General Technical  
 1322 Report SRS-54, USDA Forest Service, Asheville, NC
- 1323 Wehncke EV, Dominguez CA (2007) Seed dispersal Ecol of non-restricted frugivores capuchin monkeys in  
 1324 three neotropical forests. *J Trop Ecol* 23:519–528
- 1325 White JA, Whitham TG (2000) Associational susceptibility of cottonwood to a box elder herbivore. *Ecology*  
 1326 81:1795–1803
- 1327 Wilson MW, Irwin S, Norriss DW, Newton SF, Collins K, Kelly TC, O’Halloran J (2009) The importance of  
 1328 pre-thicket conifer plantations for nesting Hen Harriers *Circus cyaneus* in Ireland. *Ibis* 151:332–  
 1329 343
- 1330 Winfree R, Griswold T, Kremen C (2007) Effect of human disturbance on bee communities in a forested  
 1331 ecosystem. *Conserv Biol* 21:213–223
- 1332 Wolf A, Møller PF, Bradshaw RHW, Bigler J (2004) Storm damage and long-term mortality in a semi-  
 1333 natural, temperate deciduous forest. *For Ecol Manage* 188:197–210
- 1334 Zandersen M, Termansen M (2012) TEEB Nordic case: Assessing recreational values of Danish forests to  
 1335 guide national plans for afforestation. In: Kettunen M, Vihervaara P, Kinnunen S, D’Amato D,  
 1336 Badura T, Argimon M, Ten Brink P (eds) Socio-economic importance of ecosystem services in the  
 1337 Nordic Countries – Scoping assessment in the context of The Economics of Ecosystems and  
 1338 Biodiversity (TEEB). Nordic Council of Ministers, Copenhagen
- 1339 Zhao J, Wan S, Fu S, Wang X, Wang M, Liang C, Chen Y, Zhu X (2013) Effects of understory removal and  
 1340 nitrogen fertilization on soil microbial communities in *Eucalyptus* plantations. *For Ecol Manage*  
 1341 310:80–86
- 1342 Zvereva EL, Zverev V, Kozlov MV (2012) Little strokes fell great oaks: minor but chronic herbivory  
 1343 substantially reduces birch growth. *Oikos* 121:2036–2043
- 1344
- 1345
- 1346

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

<b>Section</b>	<b>Division</b>	<b>Class (with examples)</b>	<b>Number of publications</b>
<b>Provisioning</b>	<i>Nutrition</i>	Wild plants (berries, mushrooms) and animals (game) for food	2
		Water for drinking	2
<b>Regulating</b>	<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	
<b>Cultural</b>	<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

1351

1352



1354 **Box 1**

1355

1356

1357 **Box 1 – Glossary**

1358

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**

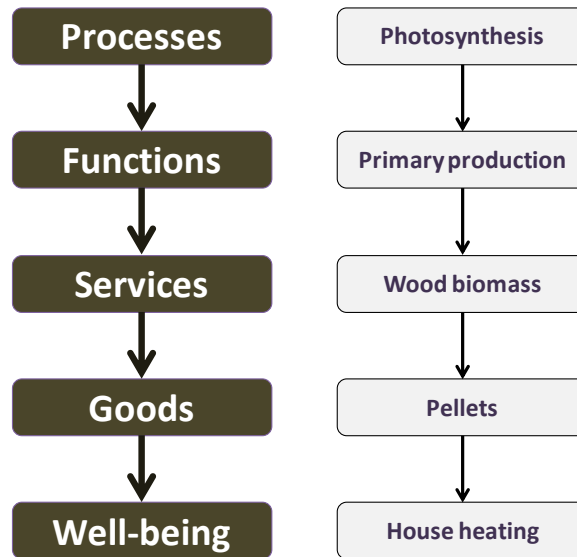
1380 Ecosystem goods are the products or benefits people can derive from final ecosystem services. Their value  
1381 is not solely provided by ecosystems and may involve additional inputs from society, for example through  
1382 human transformation or engineering. These goods may be material or immaterial, 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.

1388  
1389

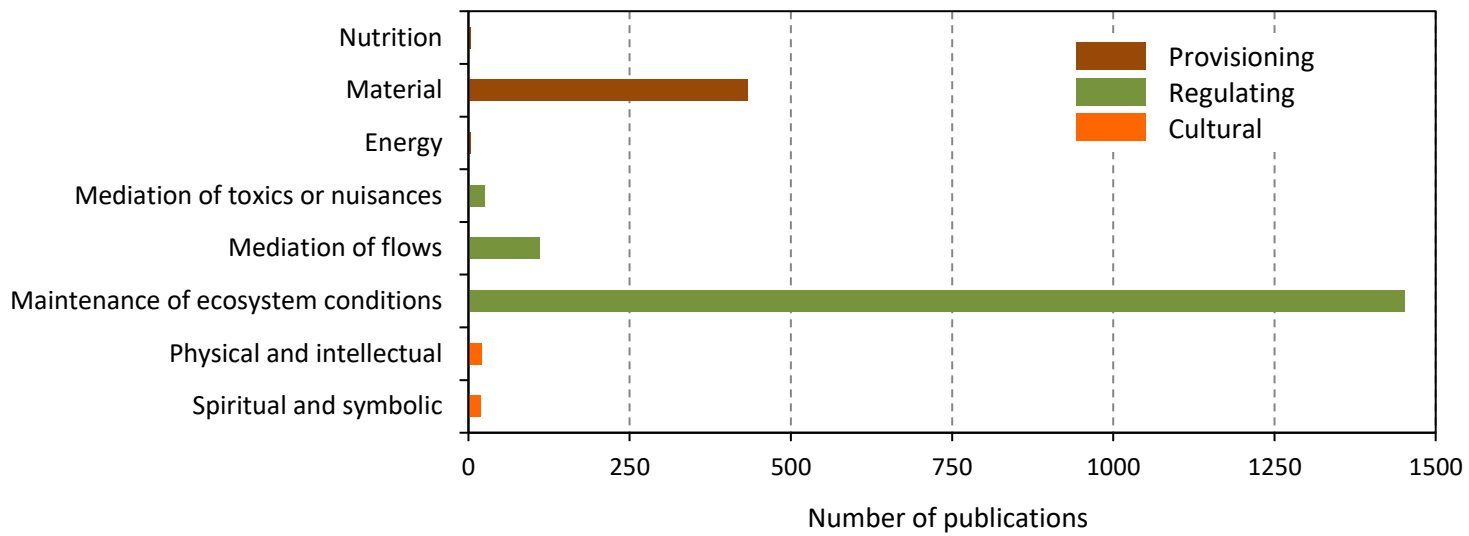


1390  
1391  
1392  
1393  
1394

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

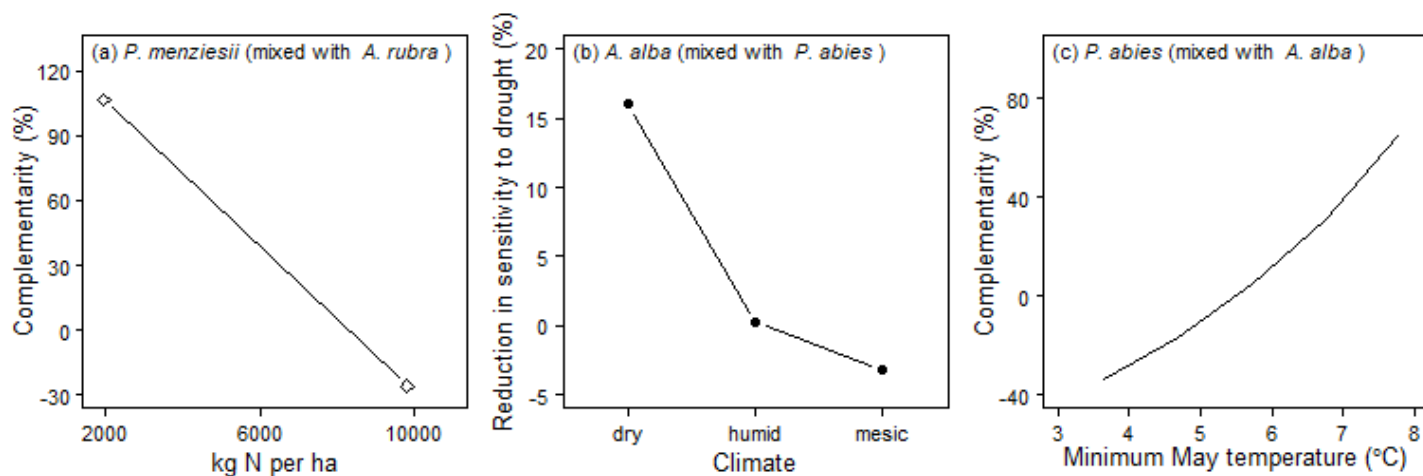
1395  
1396  
1397  
1398

1399 **Figures and captions**  
1400



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).  
1404  
1405

1406  
1407



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).  
1414  
1415