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## High ecosystem service delivery potential of small woodlands in agricultural landscapes

Alicia Valdés, Jonathan Roger Michel Henri Lenoir, Pieter de Frenne, Emilie Andrieu, Jorg Brunet, Olivier Chabrerie, Sara A. O. Cousins, Marc Deconchat, Pallieter de Smedt, Martin Diekmann, et al.

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3 AUTHOR LIST: Alicia Valdés<sup>1\*†</sup>, Jonathan Lenoir<sup>1\*</sup>, Pieter De Frenne<sup>2\*</sup>, Emilie Andrieu<sup>3</sup>,  
4 Jörg Brunet<sup>4</sup>, Olivier Chabrierie<sup>1</sup>, Sara A. O. Cousins<sup>5</sup>, Marc Deconchat<sup>3</sup>, Pallieter De Smedt<sup>2</sup>,  
5 Martin Diekmann<sup>6</sup>, Steffen Ehrmann<sup>7</sup>, Emilie Gallet-Moron<sup>1</sup>, Stefanie Gärtner<sup>7</sup>, Brice  
6 Giffard<sup>3</sup>, Karin Hansen<sup>8</sup>, Martin Hermy<sup>9</sup>, Annette Kolb<sup>6</sup>, Vincent Le Roux<sup>1</sup>, Jaan Liira<sup>10</sup>,  
7 Jessica Lindgren<sup>5</sup>, Ludmilla Martin<sup>1</sup>, Tobias Naaf<sup>11</sup>, Taavi Paal<sup>10</sup>, Willem Proesmans<sup>2</sup>,  
8 Michael Scherer-Lorenzen<sup>7</sup>, Monika Wulf<sup>11</sup>, Kris Verheyen<sup>2\*\*</sup>, Guillaume Decocq<sup>1\*\*</sup>.

9 \*These authors contributed equally to the work

10 \*\*Shared last authorship

11 †Corresponding author, e-mail: [aliciavaldes1501@gmail.com](mailto:aliciavaldes1501@gmail.com), present affiliations: Department  
12 of Ecology, Environment and Plant Sciences, Stockholm University, Svante Arrhenius väg 20  
13 A, SE-106 91 Stockholm, Sweden & Bolin Centre for Climate Research, Stockholm  
14 University, Stockholm, Sweden

15 Author affiliations:

16 <sup>1</sup>“Ecologie et Dynamique des Systèmes Anthropisés” (EDYSAN, UMR CNRS 7058), Jules  
17 Verne University of Picardie, 1 rue des Louvels, F-80037 Amiens Cedex 1, France, <sup>2</sup>Forest &  
18 Nature Lab, Ghent University, Geraardsbergsesteenweg 267, B-9090 Melle-Gontrode,  
19 Belgium, <sup>3</sup>UMR 1201 DYNAFOR, INRA, Chemin de Borde Rouge, CS 52627 F-31326  
20 Castanet, France, <sup>4</sup>Southern Swedish Forest Research Centre, Swedish University of  
21 Agricultural Sciences, Box 49, SE-230 53 Alnarp, Sweden, <sup>5</sup>Landscape Ecology, Department  
22 of Geography and Quaternary Geology, Stockholm University, SE-106 91 Stockholm,  
23 Sweden, <sup>6</sup>Vegetation Ecology and Conservation Biology, Institute of Ecology, FB2,  
24 University of Bremen, Leobener Strasse, D-28359 Bremen, Germany, <sup>7</sup>Chair of Geobotany,

25 Faculty of Biology, University of Freiburg, Schaezlestrasse 1, 79104 Freiburg, Germany,  
26 <sup>8</sup>IVL Swedish Environmental Research Institute, Box 210 60, S-100 31 Stockholm, Sweden,  
27 <sup>9</sup>Division Forest, Nature and Landscape Research, University of Leuven (KU Leuven),  
28 Celestijnenlaan 200E, B-3000 Leuven, Belgium, <sup>10</sup>Institute of Ecology and Earth Sciences,  
29 University of Tartu, Lai 40, EE-51005 Tartu, Estonia, <sup>11</sup>Leibniz-ZALF (e.V.), Institute of  
30 Land Use Systems, Eberswalder Strasse 84, D-15374 Müncheberg, Germany.

## 31 ABSTRACT

- 32 1. Global forest loss and fragmentation have strongly increased the frequency of forest  
33 patches smaller than a few hectares. Little is known about the biodiversity and  
34 ecosystem service supply potential of such small woodlands in comparison to larger  
35 forests. As it is widely recognized that high biodiversity levels increase ecosystem  
36 functionality and the delivery of multiple ecosystem services, small, isolated  
37 woodlands are expected to have a lower potential for ecosystem service delivery than  
38 large forests hosting more species.
- 39 2. We collected data on the diversity of six taxonomic groups covering invertebrates,  
40 plants and fungi, and on the supply potential of five ecosystem services and one  
41 disservice within 224 woodlands distributed across temperate Europe. We related their  
42 ability to simultaneously provide multiple ecosystem services (multiservice delivery  
43 potential) at different performance levels to biodiversity of all studied taxonomic  
44 groups (multidiversity), forest patch size and age, as well as habitat availability and  
45 connectivity within the landscape, while accounting for macroclimate, soil properties  
46 and forest structure.
- 47 3. Unexpectedly, despite their lower multidiversity, smaller woodlands had the potential  
48 to deliver multiple services at higher performance levels per area than larger  
49 woodlands of similar age, probably due to positive edge effects on the supply potential  
50 of several ecosystem services.
- 51 4. Biodiversity only affected multiservice delivery potential at a low performance level  
52 as well as some individual ecosystem services. The importance of other drivers of  
53 ecosystem service supply potential by small woodlands in agricultural landscapes also

54 depended on the level of performance and varied with the individual ecosystem  
55 service considered.

56 5. *Synthesis and applications*: Though large, ancient woodlands host the highest  
57 biodiversity and hence, can deliver a number of ecosystem services, smaller  
58 woodlands in agricultural landscapes, especially ancient woodlands, have a higher  
59 potential to deliver multiple ecosystem services on a per area basis. Despite their  
60 important contribution to agricultural landscape multifunctionality, these small  
61 woodlands are currently not considered by public policies. There is thus an urgent  
62 need for targeted policy instruments ensuring their adequate management and future  
63 conservation in order to either achieve multiservice delivery at high levels or to  
64 maximize the delivery of specific ecosystem services.

65 KEYWORDS: Anthropocene, biodiversity, connectivity, habitat fragmentation, island  
66 biogeography, management practices, metacommunity dynamics, multifunctionality,  
67 woodlands

## 68 INTRODUCTION

69 Forests deliver a wide range of ecosystem services to human society, and positive  
70 relationships between biodiversity and these services have been reported for large forested  
71 areas (Gamfeldt et al., 2013; van der Plas et al., 2016). However, there is a lack of knowledge  
72 about the relationship between biodiversity and multiple ecosystem services in small  
73 woodland patches (Decocq et al., 2016; Mitchell, Bennett, & Gonzalez, 2014). Indeed, in  
74 many parts of the world, the original forest cover has been heavily fragmented (Haddad et al.,  
75 2015; Hansen et al., 2013) due to human activities; more than 70% of the remaining global  
76 forest cover lies within 1 km of a forest edge (Haddad et al., 2015). Many of the remaining  
77 woodlands are smaller than 10 ha (Estreguil, Caudullo, de Rigo, & San Miguel, 2013) and  
78 scattered in a human-transformed matrix of mostly arable lands, pastures and human  
79 settlements. Loss of area, increased isolation and greater exposure to human disturbances  
80 along forest edges are leading causes of biodiversity loss (Haddad et al., 2015), although  
81 small patch size can sometimes be beneficial for biodiversity, as shown by the preponderance  
82 of positive significant responses to habitat fragmentation (Fahrig, 2017).

83 Small woodland patches in agricultural landscapes also vary in age, since many of  
84 them have developed on farmland that was abandoned at different points in time (Flinn &  
85 Vellend, 2005). Consequently, small woodlands not only differ in size and degree of isolation,  
86 but also in age, quantified as the time since forest establishment, ranging from very ancient  
87 (several centuries or older) to more recent (less than a century). Despite their small size and  
88 isolation, patches of (semi-)natural habitats such as small and ancient woodlands can have an  
89 important role as refugia for biodiversity (Decocq et al., 2016) and as providers of multiple  
90 ecosystem services (Decocq et al., 2016; Mitchell et al., 2014). Therefore, small and ancient  
91 forest patches, analogously to other “small natural features” (Hunter, 2017) such as scattered  
92 and old trees in agricultural landscapes (Herrera & García, 2009; Manning, Gibbons, &

93 Lindenmayer, 2006; Manning, Fischer, & Lindenmayer, 2009), have an important  
94 conservation value. This suggests that the age of these elements in the landscape might also  
95 contribute to their conservation value. As it is unknown if the relationships among  
96 biodiversity and ecosystem services that emerged from research in large forests (Gamfeldt et  
97 al., 2013; van der Plas et al., 2016) apply to small and ancient woodlands, the conservation  
98 and management of such elements in agricultural landscapes would strongly benefit from a  
99 specific assessment of the drivers of biodiversity and ecosystem service delivery in small  
100 woodlands.

101         The delivery potential of multiple ecosystem services by small and ancient woodlands  
102 can be studied by linking the theory of island biogeography (MacArthur & Wilson, 1967) to  
103 ecosystem functioning (Fig. 1). Large and spatially well-connected forest patches are  
104 expected to host more species compared to small and isolated woodlands (MacArthur &  
105 Wilson, 1967). Likewise, patches that have been forested for a long time will likely be more  
106 species-rich than recently established forests, which can remain floristically impoverished for  
107 centuries (De Frenne et al., 2011) because of the slow immigration rate of forest specialists  
108 (Naaf & Kolk, 2015). Together with this variation in taxonomic diversity (Valdés et al.,  
109 2015), the functional diversity of patches is expected to vary as well since traits of species  
110 colonizing and persisting in, for instance, small, young or isolated patches will differ from  
111 those inhabiting large, ancient or well-connected patches (Craven, Filotas, Angers, & Messier,  
112 2016; Vanneste et al., 2019). These functional responses to patch characteristics can in turn  
113 affect their functioning and potential for ecosystem service delivery (cf. Suding et al. 2008).  
114 Indeed, the effect of taxonomic or functional diversity on ecosystem functioning and service  
115 delivery is widely acknowledged and very well documented in the scientific literature  
116 (Balvanera et al., 2006; Balvanera et al., 2013; Bastian 2013; Gamfeldt et al., 2013; Lefcheck  
117 et al., 2015; van der Plas et al., 2016; Duffy, Godwin, & Cardinale, 2017). In a rigorous

118 quantitative review covering 446 measures of biodiversity effects on ecosystem functioning  
119 and services, Balvanera et al. (2006) found clear evidence that biodiversity has positive  
120 effects on most of the ecosystem services assessed in their quantitative review. Similarly, a  
121 more recent quantitative review focusing on 67 field studies has demonstrated that biomass  
122 production, a key ecosystem service, increases with species richness in a wide range of wild  
123 taxa and ecosystems (Duffy, Godwin, & Cardinale, 2017). This positive relationship between  
124 biodiversity and the delivery of single ecosystem services has even been extended to the  
125 delivery of multiple services (Gamfeldt et al., 2013; van der Plas et al., 2016; Lefcheck et al.,  
126 2015). For instance, higher levels of multiple ecosystem services are found in large forests  
127 with more tree species (Gamfeldt et al., 2013). If the positive relationship between  
128 biodiversity and the delivery of multiple ecosystem services reported for large forested areas  
129 (Gamfeldt et al., 2013; van der Plas et al., 2016) would be fully applicable to small  
130 woodlands, we could hypothesize that small, isolated and recent woodlands (cf. situation “a”  
131 in Fig. 1) would have a lower ecosystem service supply potential (Bodin, Tengö, Norman,  
132 Lundberg, & Elmqvist, 2006; Decocq et al., 2016), because they harbor less biodiversity  
133 compared to large, connected and ancient forest patches (cf. situation “d” in Fig. 1).

134         Here, we assess the supply potential of multiple ecosystem services provided by small  
135 (both recent and ancient) woodlands as well as larger (both recent and ancient) forest patches  
136 ( $n = 224$ ) in agricultural landscapes distributed along a 2500-km latitudinal gradient spanning  
137 the entire temperate forest biome in Europe (Fig. 2). We collected biodiversity data for six  
138 taxonomic groups with different functional roles and dispersal potential, as well as data on the  
139 supply potential of six important ecosystem (dis)services delivered by woodlands,  
140 representing a mixture of provisioning, regulating and cultural services.

## 141 MATERIALS AND METHODS

### 142 **Study area and sampling design**

143 We studied deciduous forest patches in seven regions along a transect spanning *c.* 2500 km  
144 across the entire temperate forest biome of Europe (Fig. 2). In each region, two  $5 \times 5$  km<sup>2</sup>  
145 landscape windows (14 in total) with two contrasting connectivity levels were selected: (1) a  
146 “high-disturbance landscape” with isolated forest patches surrounded by an intensively  
147 cultivated matrix, dominated by large open fields with intensive use of pesticides and  
148 fertilizers; and (2) a “low-disturbance landscape” with forest patches more or less connected  
149 by different types of hedgerows and surrounded by a less disturbed matrix with fewer and  
150 smaller crop fields (see Valdés et al. (2015) for more info). In each landscape window, sixteen  
151 woodlands were selected for sampling. When possible, these woodlands were chosen to be  
152 equally distributed among each of four combinations of size and historical age categories:  
153 small-old, small-young, large-old, large-young (see details on patch selection in Appendix S1,  
154 and summary statistics for each size and age category per landscape window in Table S1).

## 155 **Data collection**

### 156 *Patch features*

157 Patch size and historical age were calculated with a geographic information system (GIS,  
158 ArcGis 9.3, ESRI), using contemporary and historical maps of the landscape windows (recent  
159 aerial photographs, all taken after the year 2000, and maps from the 18th, 19th and 20th  
160 centuries). Patch size was calculated using digitized woodlands in each window. For  
161 calculating patch historical age, we digitized all woodlands in historical maps, and historical  
162 age was estimated using the date of the oldest map on which a patch appeared. As a given  
163 patch may contain a mosaic of fragments with different historical ages, we calculated a size-  
164 weighted average of the historical age of all fragments composing an isolated patch.

165 We used a 500-m buffer centered on each patch to calculate metrics related to habitat  
166 connectivity (see also Valdés et al., 2015) and the habitat amount hypothesis *sensu* Fahrig

167 (Fahrig, 2013): (1) the proportion of buffer surface covered by forest, with higher values  
168 indicating a higher amount of forest habitat availability within the landscape; and (2) the  
169 proportion of buffer surface covered by crops, with higher values indicating a lower habitat  
170 connectivity, as agricultural intensification of the matrix reduces forest connectivity and  
171 increases its ecological isolation (Donald & Evans, 2006).

## 172 *Environmental drivers*

173 We calculated values of three groups of environmental drivers that can affect both  
174 biodiversity and supply potential of multiple ecosystem services: macroclimatic, soil and  
175 forest structural drivers.

### 176 *Macroclimatic drivers*

177 We extracted five temperature variables from the EuroLST dataset (250-m resolution,  
178 <http://www.geodati.fmach.it/eurolst.html>) and five precipitation variables from the  
179 WorldClim global database (1-km resolution, <http://www.worldclim.org/>) and averaged each  
180 variable for each patch using all pixels intersecting with the patch area. We performed a  
181 principal components analysis (PCA, Fig. S1) on these 10 variables representing seasonality  
182 and extreme or limiting environmental factors (see details on Fig. S1 legend), and retained the  
183 first axis (explaining 74% of the total variance) as an explanatory variable in our models. This  
184 variable, called “macroclimate”, indicated high seasonality and low temperature and  
185 precipitation.

### 186 *Soil drivers*

187 We took soil samples in each patch (see details on soil sampling in Appendix S1), and  
188 calculated mean values of depth of the forest floor, C:N ratio, total P content and pH of the  
189 mineral topsoil at the patch level and used them to perform a PCA (Fig. S2). We then retained  
190 axes 1 and 2 (explaining, respectively, 44 and 26 % of the total variance) as explanatory

191 variables in our models. Axis 1, called “soil nutrients”, was positively correlated with the total  
192 P in the mineral topsoil and negatively correlated with the depth of the forest floor. Axis 2,  
193 called “soil acidity & C/N” was positively correlated with the C:N ratio in the mineral topsoil  
194 and negatively correlated with the pH of the mineral topsoil.

#### 195 *Forest structural drivers*

196 We calculated two variables describing variation in forest composition and structure,  
197 respectively: tree diversity, calculated as a stem number-based Shannon diversity index; and  
198 structural diversity, calculated as the coefficient of variation (CV) of tree diameters (see  
199 details on data collection in Appendix S1). These variables were selected based on data  
200 availability on the one hand and their relevance for explaining variation in tree and forest-  
201 associated biodiversity and in ecosystem functioning (e.g. van der Plas et al., 2016 and  
202 Penone et al., 2019) on the other hand.

#### 203 ***Biodiversity***

204 In order to assess patch biodiversity (hereafter multidiversity *sensu* Allan et al. 2014), we  
205 surveyed species richness for six different taxonomic groups that are representative of forest-  
206 associated ground-dwelling biota: ground beetles (i.e. Insecta); spiders (i.e. Arachnida);  
207 millipedes (i.e. Myriapoda); woodlice (i.e. Crustacea); understory herbs (i.e. focusing on  
208 vascular plant species only); and mushrooms (i.e. focusing on species with visible and above-  
209 ground fruiting bodies such as stem, cap and gills). The selected groups cover different  
210 trophic levels (primary producers, predators and decomposers) and are assumed to directly or  
211 indirectly influence the potential delivery of the six studied ecosystem services. We refer to  
212 Appendix S1 for more information on field surveys specific to each taxonomic group.

#### 213 ***Proxies for supply potential of multiple ecosystem services***

214 In addition to patch multidiversity, we assessed the potential of a given patch to  
 215 simultaneously provide multiple services (hereafter multiservice delivery potential). Here we  
 216 included two proxies for provisioning services (abundance of usable plants and stemwood  
 217 volume), three for regulating services (pest control potential, tick-borne disease risk and  
 218 topsoil carbon storage), and one for a cultural or recreational service (game production  
 219 potential). See Appendix S1 for more information on each service/disservice and details on  
 220 data collection.

### 221 **Calculation of multidiversity and multiservice delivery**

222 For each patch  $i$ , we calculated a multidiversity index (MD) according to Allan et al. (2014)  
 223 using the raw species richness values of understory herbs (UH), mushrooms (MU), carabid  
 224 beetles (CB), spiders (SP), millipedes (MI) and woodlice (WO). Each raw species richness  
 225 value for a given taxonomic group was divided by the mean of the five highest values among  
 226 all studied patches to account for extreme values (Allan et al., 2014). MD was calculated as:

$$MD = average \left[ \left( \frac{UH_i}{UH_{5\text{highest}}} + \frac{MU_i}{MU_{5\text{highest}}} + \frac{CB_i}{CB_{5\text{highest}}} + \frac{SP_i}{SP_{5\text{highest}}} + \frac{MI_i}{MI_{5\text{highest}}} + \frac{WO_i}{WO_{5\text{highest}}} \right) \right]$$

227 (Equation 1)

228 Based on the raw values of each individual ecosystem service/disservice, we used a  
 229 multiple threshold approach (Byrnes et al., 2014) to define service-specific threshold values  
 230 representing low, intermediate and high performance levels of ecosystem service supply  
 231 potential (see details in Table S2). The performance level is the amount of the provided  
 232 service (or disservice) supply potential per area unit and could either be low, intermediate or  
 233 high. Examples of high performance levels are, for instance, small woodland patches that  
 234 simultaneously provide a large total stemwood volume ( $> 300 \text{ m}^3$  per ha) and have a low  
 235 density of ticks ( $< 50$  nymphs per  $100 \text{ m}^2$ ) and thus minimize the prevalence of tick-borne  
 236 diseases in the human population. For each of the three performance levels, we calculated

237 multiservice delivery potential as the proportion of ecosystem service proxies (sometimes less  
238 than six measured ecosystem proxies per patch if the data was not available for a given proxy  
239 within a focal patch) for which the amount of the provided service (or disservice) proxy per  
240 area unit exceeded (or was lower than) a proxy-dependent threshold (Table S2). For instance,  
241 if one service proxy exceeded its high-threshold value and two exceeded their respective low-  
242 threshold values within a given patch for which five services were measured in total, then the  
243 high-performance multiservice delivery potential is 0.2 and the low-performance multiservice  
244 delivery is 0.4 for this patch. This threshold approach is considered as the state-of-the-art  
245 standard method to evaluate multiservice delivery (Byrnes et al., 2014; Gamfeldt, Hillebrand,  
246 & Jonsson, 2008; Lefcheck et al., 2015). Multiple thresholds are used because it has been  
247 shown that the sign of the relationship between biodiversity and ecosystem multifunctionality  
248 can differ when low-performance versus high-performance thresholds are applied (van der  
249 Plas et al., 2016).

## 250 **Statistical modeling**

251 We used piecewise structural equation modeling (piecewise SEM, Lefcheck, 2016) to study  
252 the response of low-, intermediate- and high-performance multiservice delivery potential to  
253 multidiversity, patch characteristics (size, age and the interaction between size and age) as  
254 well as habitat availability and connectivity within the landscape, while accounting also for  
255 macroclimate, soil and forest structural characteristics. We chose a piecewise approach  
256 (instead of the traditional variance-covariance based SEM) because of its ability to fit multiple  
257 separate linear models with non-normal distributions and random effects, which was well-  
258 suited for our data. In our models, we considered both direct responses of multiservice  
259 delivery potential to the different predictors, and indirect responses mediated by effects of the  
260 different predictors on multidiversity. The piecewise SEM consisted of four component  
261 models:

- 262 1. A linear mixed-effects model (LMM) with tree diversity as the response variable and  
263 patch size (log-transformed), historical age, habitat availability (proportion of  
264 forests) and connectivity (proportion of crops), macroclimate (PC1) and soil (PC1  
265 and PC2) as predictor variables.
- 266 2. A LMM with structural diversity as the response variable and patch size (log-  
267 transformed), historical age, habitat availability (proportion of forests) and  
268 connectivity (proportion of crops) and tree diversity as predictor variables.
- 269 3. A LMM with multidiversity as the response variable and patch size (log-  
270 transformed), historical age (and their interaction term to account for the species-  
271 time-area relationship; Adler et al. 2005), habitat availability (proportion of forests)  
272 and connectivity (proportion of crops), macroclimate (PC1), soil (PC1 and PC2), tree  
273 diversity and structural diversity as predictor variables.
- 274 4. A generalized linear mixed-effects model (GLMM) with a binomial error distribution  
275 with multiservice delivery potential as the response variable and multidiversity, patch  
276 size (log-transformed), historical age, habitat availability (proportion of forests) and  
277 connectivity (proportion of crops), macroclimate (PC1), soil (PC1 and PC2), tree  
278 diversity and structural diversity as predictor variables.

279 LMMs were used for response variables with approximately normal distributions (tree  
280 diversity, structural diversity and multidiversity), and a binomial GLMM was used for  
281 multiservice delivery potential (proportional). We used “region” and “window type” nested  
282 within “region” as random effect terms in all four component models to account for the  
283 hierarchical, nested structure of the sampling design along the studied gradient. This  
284 piecewise SEM model structure was tested for the three levels of performance of multiservice  
285 delivery potential considered (low, intermediate and high), and for each individual ecosystem

286 service, separately. Overall fit of the piecewise SEM models was assessed using Shipley's test  
287 of direct separation (Shipley, 2009), which evaluates the probability that none of the paths  
288 missing from the hypothesized causal network contain useful information, and yields the  
289 Fisher's C statistic. A  $\chi^2$ -value of Fisher's C below the significance level ( $p < 0.05$ ) indicates  
290 that the model is inconsistent with the data, and should be rejected. Statistical analyses were  
291 carried out in R 3.4.2 (R Core Team, 2018) using the packages piecewiseSEM (Lefcheck,  
292 2016) and nlme (Pinheiro, Bates, DebRoy, & Sarkar, 2016).

## 293 RESULTS

294 Tree species diversity increased with patch historical age, while structural diversity, in turn,  
295 increased with tree species diversity (Fig. 3). Multidiversity was higher in the larger and more  
296 ancient patches, as shown by the positive interaction effect ( $p = 0.03$ ) between patch size and  
297 historical age (Fig. 3).

298         The response of multiservice delivery potential to multidiversity, patch characteristics,  
299 habitat availability and connectivity and environmental drivers depended on the level of  
300 performance considered. Multiservice delivery potential at a low performance level increased  
301 with multidiversity and was also indirectly positively affected by the interaction between  
302 patch size and historical age as larger and more ancient patches hosted higher levels of  
303 multidiversity (Fig. S3). Multiservice delivery potential at an intermediate performance level  
304 was not affected by any of the studied drivers (Fig. S3). Multiservice delivery potential at a  
305 high performance level increased directly with patch historical age and decreased directly  
306 with patch size, i.e. it was maximal in the smallest and most ancient woodlands (Fig. 3). It  
307 also decreased with soil acidity & C/N, i.e. it was maximal in less acidic soils with lower C:N  
308 ratio (Fig. 3).

309 Each individual ecosystem service/disservice showed a particular response to the array  
310 of drivers studied (Fig. 4). Patch size affected three ecosystem service proxies and patch age  
311 only one. Smaller woodlands exhibited a higher game production potential and topsoil carbon  
312 storage capacity, but lower tick-borne disease risk than larger patches. More ancient  
313 woodlands showed a higher topsoil carbon storage. Multidiversity, mediated by the positive  
314 interaction effect of patch size  $\times$  patch age, had a significant positive impact on three out of  
315 the six individual ecosystem services studied: abundance of usable plants, pest control  
316 potential and game production potential, while tick-borne disease risk, topsoil carbon storage,  
317 and stemwood volume were unaffected by multidiversity. The landscape variables only had a  
318 limited effect on the ecosystem service delivery potential, with only the abundance of usable  
319 plants positively related to habitat connectivity. The abundance of usable plants was also the  
320 only service proxy affected by macroclimate; enhanced seasonality had a positive effect. Soil  
321 drivers affected several individual ecosystem services. Soil nutrient availability increased the  
322 abundance of usable plants and decreased tick-borne disease risk, game production potential  
323 and topsoil carbon storage. Tick-borne disease risk and game production potential increased  
324 in more acidic soils with higher C:N ratio, while the abundance of usable plants and  
325 stemwood volume decreased. Forest structure affected two proxies: game production potential  
326 increased with tree species diversity and decreased with structural diversity, and stemwood  
327 volume, which decreased with tree species diversity and increased with structural diversity.  
328 All piecewise SEM models reported here were consistent with the data ( $p > 0.05$  in all cases).

## 329 DISCUSSION

330 We showed that multidiversity was highest in large and ancient forest patches. Multiservice  
331 delivery potential at high performance levels per area was maximal in the smallest and most  
332 ancient woodlands and was not affected by multidiversity, which only influenced multiservice

333 delivery potential at low performance levels, as well as some of the individual ecosystem  
334 services.

335 *The interplay between patch biodiversity, age and size and their effects on multiservice*  
336 *delivery potential*

337 Our results show that, although larger and more ancient woodlands hosted a higher  
338 biodiversity, as predicted by the species-time-area relationship (Adler et al., 2005), this was  
339 unrelated to a high-performance multiservice delivery potential. Contrary to our expectations,  
340 high-performance multiservice delivery potential decreased as patch size increased,  
341 independent of the positive effect of patch size on multidiversity. This means that smaller  
342 woodlands potentially deliver multiple services at higher performance levels on a per area  
343 basis than larger woodlands of a similar age, even if the larger woodlands harbor a higher  
344 biodiversity. This unexpected result may be explained by the positive edge effect on the  
345 delivery potential of some ecosystem services (Bodin et al., 2006; Mitchell et al., 2014). As  
346 smaller woodlands have a relatively high edge-to-core ratio (Ewers & Banks-Leite, 2013;  
347 Weathers, Cadenasso, & Pickett, 2001), they are highly exposed to external influences; they  
348 receive, for example, proportionally more light penetrating through the edge, a warmer and  
349 drier microclimate and more nutrient input from surrounding agricultural lands compared to  
350 large forests. These conditions promote, among others, higher patch-level microclimate  
351 heterogeneity (Frey et al., 2016) as well as a more dense vegetation cover and an increased  
352 biomass production at forest edges (Remy, Wuyts, Van Nevel, et al., 2018; Remy, Wuyts,  
353 Verheyen, Gundersen, & Boeckx, 2018) in small woodlands. This altered functioning in turn  
354 increases the delivery potential of some services, such as game production potential, due to an  
355 increased quantity of food available for game, and topsoil carbon storage, due to the faster  
356 incorporation of organic matter in the soil. Tick-borne disease risk is, however, lower, likely

357 due to decreased larval densities in the unfavorable (e.g. hotter and drier) microclimatic  
358 conditions at the edge (Ehrmann et al., 2017).

359         On the other hand, the positive and indirect interaction effect of patch size and age,  
360 mediated by a higher multidiversity, increased multiservice delivery potential at a low-  
361 performance level, as well as some individual ecosystem services. Therefore, it seems that the  
362 higher biodiversity hosted by larger and more ancient woodlands is able to maintain a  
363 minimal level of multiservice supply potential, while the maintenance of higher levels is less  
364 dependent on the amount of biodiversity. The supply potential of several individual ecosystem  
365 services indirectly increased in larger and more ancient woodlands because it was dependent  
366 on higher levels of biodiversity. For example, abundance of usable plants and game  
367 production potential might have increased due to a positive correlation with vascular plant  
368 diversity, while pest control potential probably increased due to bottom-up effects through the  
369 trophic chain (Scherber et al., 2010). On the contrary, tick-borne disease risk, topsoil carbon  
370 storage and stemwood volume were unrelated to multidiversity, probably because they  
371 depended on particular environmental conditions or on the presence and abundance of  
372 specific species (Winfree, Fox, Williams, Reilly, & Cariveau, 2015) rather than on species  
373 richness *per se*.

374         Finally, it should be noted that we focused on the service delivery potential on a per  
375 area basis and that the total amount of services provided by large patches might still be larger  
376 than that of small patches. Our findings should therefore not be interpreted as a trade-off  
377 between large, biodiverse patches versus small patches that have a higher potential to deliver  
378 services, but rather as an observation that small woodlands in agricultural landscapes have the  
379 potential to deliver a high flow of services relative to their size.

380 *The effect of other drivers on woodland multiservice delivery potential*

381 The amount of forest cover around each woodland (cf. the habitat amount hypothesis, Fahrig,  
382 2013) had no effect on multidiversity, multiservice delivery potential and individual services,  
383 which indicates that habitat availability within the landscape did not influence the service  
384 supply potential. This lack of effect may be a consequence of the disruption of  
385 metacommunity functioning in highly fragmented systems, with the dispersal of species  
386 among small forest patches dramatically reduced (Jamoneau, Chabrerie, Closset-Kopp, &  
387 Decocq, 2012). Both models (Thompson & Gonzalez, 2016) and experiments (Haddad et al.,  
388 2015) predict reduced multifunctionality in such highly fragmented systems. The delivery of  
389 some ecosystem services may decline with low habitat connectivity, and with an intensively  
390 managed landscape matrix, as we have observed for the abundance of usable plants, which  
391 decreased with the proportion of crops surrounding the forest patch. Such an effect most  
392 likely results from a greater exposure of the forest edges to the biocides and fertilizers used in  
393 the adjacent croplands (Chabrerie, Jamoneau, Gallet-Moron, & Decocq, 2013).

394         Macroclimatic conditions affected neither multidiversity nor multiservice delivery  
395 potential, although we studied a large climatic gradient covering the entire European  
396 temperate biome. Only one of the individual services, the abundance of usable plants, was  
397 positively affected by macroclimate seasonality, increasing towards northern latitudes. This  
398 overall lack of effects of macroclimate suggests that the expected major biogeographic  
399 gradients influencing ecosystem service delivery potential are lost in highly fragmented forest  
400 ecosystems, at least partly due to the loss of macroclimate-driven biodiversity gradients  
401 (Valdés et al., 2015, Vanneste et al., 2019) and a decoupling between sub-canopy and free-air  
402 temperatures (De Frenne et al., 2013, 2019; Frey et al., 2016; Lenoir, Hattab, & Pierre, 2017).  
403 Similarly, other potentially influential microclimate factors such as soil moisture and relative  
404 air humidity, not assessed in this study, could contribute to the observed lack of effects of  
405 macroclimate on multidiversity and multiservice delivery.

#### 406 *Future research avenues*

407 This study is a first step towards a better understanding of the factors that influence the  
408 biodiversity and multiservice delivery potential of woodland patches in agricultural  
409 landscapes. Obviously, not all possible services were considered here (see Decocq et al. 2016  
410 for an overview) and this raises the question of whether inclusion of other services, like  
411 erosion control and water quality regulation, both acting at a landscape scale, would alter the  
412 results. This is not unlikely, since it has been shown that different services are underpinned by  
413 different forest attributes (Felipe-Lucia et al., 2018). Next, inclusion of more driving  
414 variables, e.g. those that quantify the past and current management and the microclimate in  
415 the patches, may help to further clarify how human actions in these patches influence their  
416 biodiversity and ecosystem service delivery potential. Another research avenue along the  
417 same lines is making the step from ecosystem service delivery potential towards actual  
418 ecosystem delivery. Indeed, not all services play an equally important role in all landscapes or  
419 for all stakeholders, and potential ecosystem service assessments should ideally be  
420 complemented by socio-economic analyses quantifying the importance and value of the  
421 studied services (e.g. Bagstad et al., 2014; Zoderer et al., 2019). Finally, such integrated  
422 analyses will require the use of more sophisticated indicators that better reflect the actual  
423 ecosystem services that are delivered than the indicators we used.

#### 424 CONCLUSIONS

425 Our study responds to the call for empirical research into the nature of the relationships  
426 between fragmentation and ecosystem service supply potential (Mitchell et al., 2015). We  
427 have shown that both large and small woodland patches in agricultural landscapes fulfill  
428 important roles. The large, ancient woodlands host the highest biodiversity and are  
429 particularly important for conservation. They also have the potential to deliver a considerable  
430 flow of services, but smaller woodlands have a higher potential to deliver multiple ecosystem

431 services on a per area basis than the larger woodlands, especially when they are ancient. This  
432 higher potential of small woodlands might be caused by edge effects that can enhance the  
433 delivery potential of several services. Preserving the small woodlands is hence important to  
434 increase the multifunctionality of agricultural landscapes. This is an important finding  
435 because especially the small woodlands are currently not included in major national and  
436 international policies affecting biodiversity and ecosystem services in agricultural landscapes,  
437 such as the EU Natura 2000 network, the EU water Directive and the Common Agricultural  
438 Policy (Pe'er et al., 2014). Our findings advocate for the development of relevant policy  
439 instruments in order to ensure their future conservation. Next, we also found that the  
440 importance of drivers vary depending on performance levels of the ecosystem service and on  
441 the individual (dis-)service considered. A given driver may thus affect individual services in  
442 opposite directions, which leads to trade-offs among services (Gamfeldt et al., 2013; Lefcheck  
443 et al., 2015; Felipe-Lucia et al., 2018). Consequently, different management strategies of  
444 these woodlands would be required to achieve multiservice delivery at high performance  
445 levels or to maximize (respectively minimize) the delivery of a specific ecosystem service  
446 (respectively disservice). For some services and performance levels, biodiversity conservation  
447 and ecosystem service delivery go hand in hand, but in other cases there may be a trade-off  
448 between both. This should be taken into account when designing policies and management  
449 strategies for small woodlands in agricultural landscapes.

#### 450 AUTHORS' CONTRIBUTIONS

451 Author contributions: AV, JL and PDF contributed equally to the work. KV and GD share the  
452 last authorship. AV, JL, PDF, KV and GD designed the study. All authors collected the data.  
453 JL, AV, PDF and KV analyzed the data. AV, JL, PDF, KV and GD wrote the first draft of the  
454 paper. All authors contributed substantially to the writing and gave final approval for  
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## 468 DATA ACCESSIBILITY

469 Should the manuscript be accepted, the data supporting the results will be archived in an  
470 appropriate public repository (e.g. Dryad) and the data DOI will be included at the end of the  
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473 Figure 1: Linking island biogeography (MacArthur & Wilson, 1967) and ecosystem  
474 functioning for studying the supply potential of multiple ecosystem services by small forest  
475 patches. Hypothetical framework on the effects of forest continuity across space and over  
476 time on immigration and extinction rates, and thus on the level of biodiversity (i.e. total  
477 number of species per forest patch) and the associated supply potential of multiple ecosystem  
478 services. (A) MacArthur & Wilson's theory of island biogeography adapted to forest  
479 spatiotemporal characteristics (effect of patch connectivity and age on immigration rate and of  
480 patch size on extinction rate). (B) Theoretically expected relationship between species  
481 richness and supply potential of multiple ecosystem services. The letters along the x-axis (a,  
482 b, c and d) depict different landscapes with different expectations on species richness and thus  
483 on supply potential of multiple ecosystem services, consisting of: (a) small, isolated and  
484 recent forest patches (a lower species richness is expected); (b) large but isolated and recent  
485 forest patches (intermediate levels of species richness are expected); (c) small but connected  
486 and ancient forest patches (intermediate levels of species richness are expected); and (d) large,  
487 connected and ancient forest patches (a higher species richness is expected). The green line  
488 and the green shaded polygon depict the average expected relationship between species  
489 richness and supply potential of multiple ecosystem services as well as the hypothetic  
490 confidence interval of all possible shapes we can expect for this relationship, respectively.

491 Figure 2: Sampling biodiversity and ecosystem service supply potential in small forest  
492 patches in agricultural landscapes. (A) Sampling locations along the 2500-km latitudinal  
493 gradient in Europe (SF = South France, NF = North France, BE = Belgium, WG = West  
494 Germany, EG = East Germany, SS = South Sweden, CS = Central Sweden). (B) Detail of two  
495 of the 14 studied landscapes (low vs. high connectivity) in North France, showing the  
496 distribution of land uses and the selected forest patches in red. Each landscape is  $5 \times 5 \text{ km}^2$ .

497 (C) Detail of the six taxonomic groups, six ecosystem services (blue) or disservices (red) and  
498 four groups of drivers assessed within each of the selected forest patches.

499 Figure 3: Linkage between the environment, biodiversity and high-performance multiservice  
500 delivery potential in small woodlands across Europe. Results of the piecewise structural  
501 equation model ( $p = 0.512$ ) studying the response of high-performance multiservice delivery  
502 potential to multidiversity, patch size, age and connectivity (proportion of forests and crops in  
503 a 500-m surface around each patch), while accounting for macroclimate, soil and forest  
504 structural characteristics as environmental drivers. Blue arrows indicate positive effects and  
505 red arrows indicate negative effects. Arrow thickness is proportional to the effect size. Only  
506 significant paths ( $p < 0.05$ ) are shown, while variables not significantly contributing to the  
507 models are attenuated and represented with grey shading. Grey crossed arrows have been  
508 included to highlight the lack of effects of multidiversity on multiservice, and of tree species  
509 diversity and stand structure on multidiversity. The blue square depicts the positive interaction  
510 effect ( $p = 0.03$ ) between patch size and historical age on multidiversity, as predicted by the  
511 species-time-area relationship. Marginal (i.e. fixed effects) and conditional (fixed plus random  
512 effects)  $R^2$  values are 0.33 and 0.48, respectively. The color ramp from red to blue depicts  
513 different historical patch ages ranging from the youngest (10 yrs) to the oldest (270 yrs)  
514 sampled patch ( $n = 200$ ). All covariates (connectivity, macroclimate, soil and stand  
515 conditions) in the model except patch size and historical age were set to their mean values.

516 Figure 4: Linkage between the environment, biodiversity and individual ecosystem service  
517 supply potential in small woodlands across Europe. Results of the piecewise structural  
518 equation models studying the response of each individual ecosystem service to multidiversity,  
519 patch size, historical age and connectivity (proportion of forests and crops in a 500-m surface  
520 around each patch), while accounting also for macroclimate, soil and forest structural  
521 characteristics as environmental drivers. Blue arrows indicate positive effects and red arrows

522 indicate negative effects. Arrow thickness is proportional to the effect size. Only significant  
523 paths ( $p < 0.05$ ) are shown, while variables not significantly contributing to the models are  
524 attenuated and represented with grey shading. The overall p-value for each piecewise  
525 structural equation model (piecewise SEM) is shown in the heading of each panel.

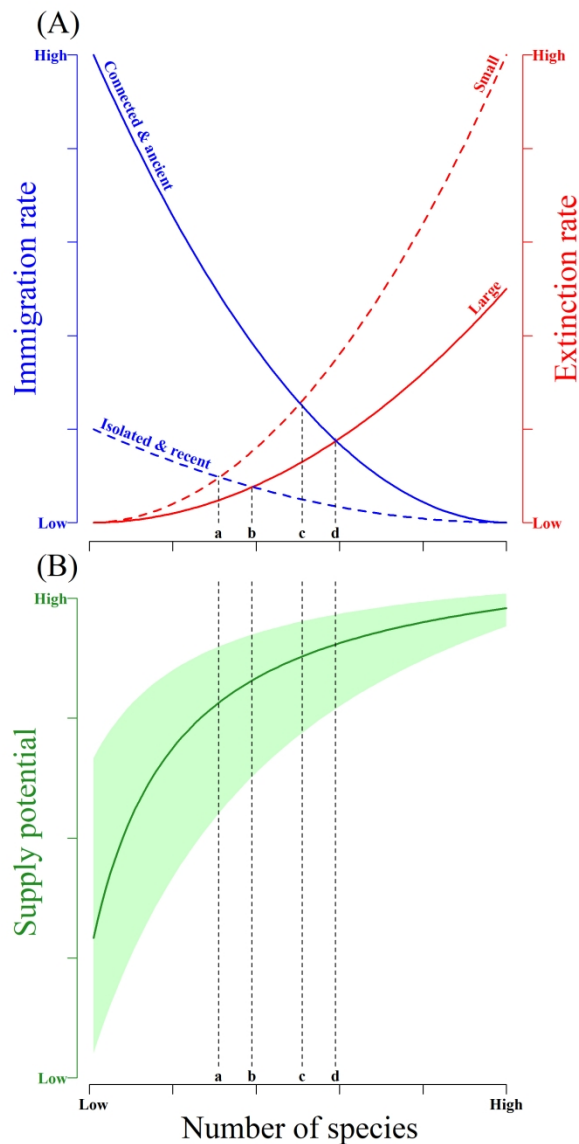


Figure 1: Linking island biogeography (MacArthur & Wilson, 1967) and ecosystem functioning for studying the supply potential of multiple ecosystem services by small forest patches. Hypothetical framework on the effects of forest continuity across space and over time on immigration and extinction rates, and thus on the level of biodiversity (i.e. total number of species per forest patch) and the associated supply potential of multiple ecosystem services. (A) MacArthur & Wilson's theory of island biogeography adapted to forest spatiotemporal characteristics (effect of patch connectivity and age on immigration rate and of patch size on extinction rate). (B) Theoretically expected relationship between species richness and supply potential of multiple ecosystem services. The letters along the x-axis (a, b, c and d) depict different landscapes with different expectations on species richness and thus on supply potential of multiple ecosystem services, consisting of: (a) small, isolated and recent forest patches (a lower species richness is expected); (b) large but isolated and recent forest patches (intermediate levels of species richness are expected); (c) small but connected and ancient forest patches (intermediate levels of species richness are expected); and (d) large, connected and ancient forest patches (a higher species richness is expected). The green line and the green shaded polygon depict the average expected relationship between species richness and supply potential of

multiple ecosystem services as well as the hypothetical confidence interval of all possible shapes we can expect for this relationship, respectively.

159x319mm (300 x 300 DPI)

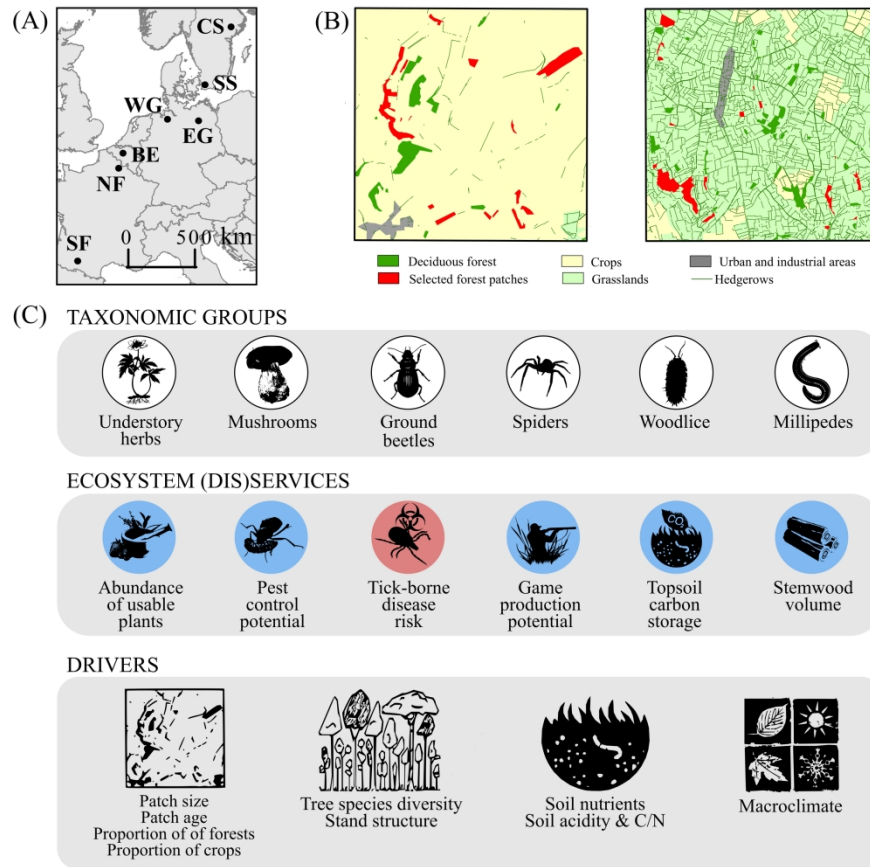


Figure 2: Sampling biodiversity and ecosystem services in small forest patches in agricultural landscapes. (A) Sampling locations along the 2500-km latitudinal gradient in Europe (SF = South France, NF = North France, BE = Belgium, WG = West Germany, EG = East Germany, SS = South Sweden, CS = Central Sweden). (B) Detail of two of the 14 studied landscapes (low vs. high connectivity) in North France, showing the distribution of land uses and the selected forest patches in red. Each landscape is 5 × 5 km<sup>2</sup>. (C) Detail of the six taxonomic groups, six ecosystem services (blue) or disservices (red) and four groups of drivers assessed within each of the selected forest patches.

245x215mm (300 x 300 DPI)

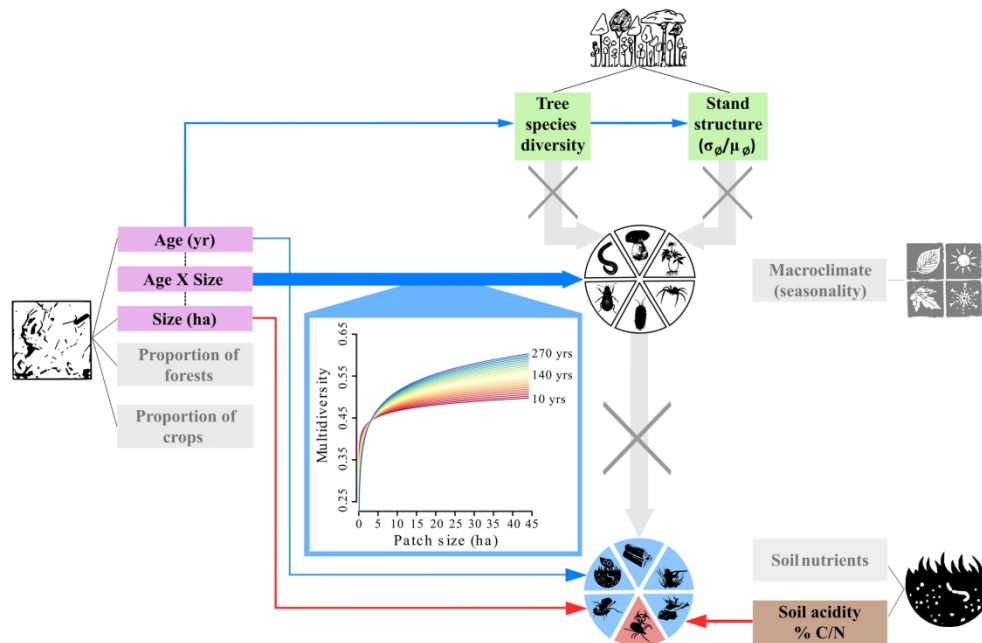


Figure 3: Linkage between the environment, biodiversity and high-performance multiservice delivery in small woodlands across Europe. Results of the piecewise structural equation model (piecewise SEM,  $p = 0.512$ ) studying the response of high-performance multiservice (MS) delivery to multidiversity, patch size, age and connectivity (proportion of forests and crops in a 500-m surface around each patch), while accounting for macroclimate, soil and forest structural characteristics as environmental drivers. Blue arrows indicate positive effects and red arrows indicate negative effects. Arrow thickness is proportional to the effect size. Only significant paths ( $p < 0.05$ ) are shown, while variables not significantly contributing to the models are attenuated and represented with grey shading. Grey crossed arrows have been included to highlight the lack of effects of multidiversity on multiservice, and of tree species diversity and stand structure on multidiversity. The blue square depicts the positive interaction effect ( $p = 0.03$ ) between patch size and historical age on multidiversity, as predicted by the species-time-area relationship. Marginal (cf. fixed effects) and conditional (fixed and random effects)  $R^2$  values are 0.33 and 0.48, respectively. The color ramp from red to blue depicts different historical patch ages ranging from the youngest (10 yrs) to the oldest (270 yrs) sampled patch ( $n = 200$ ). All covariates (connectivity, macroclimate, soil and stand conditions) in the model except patch size and historical age were set to their mean values.

181x119mm (300 x 300 DPI)

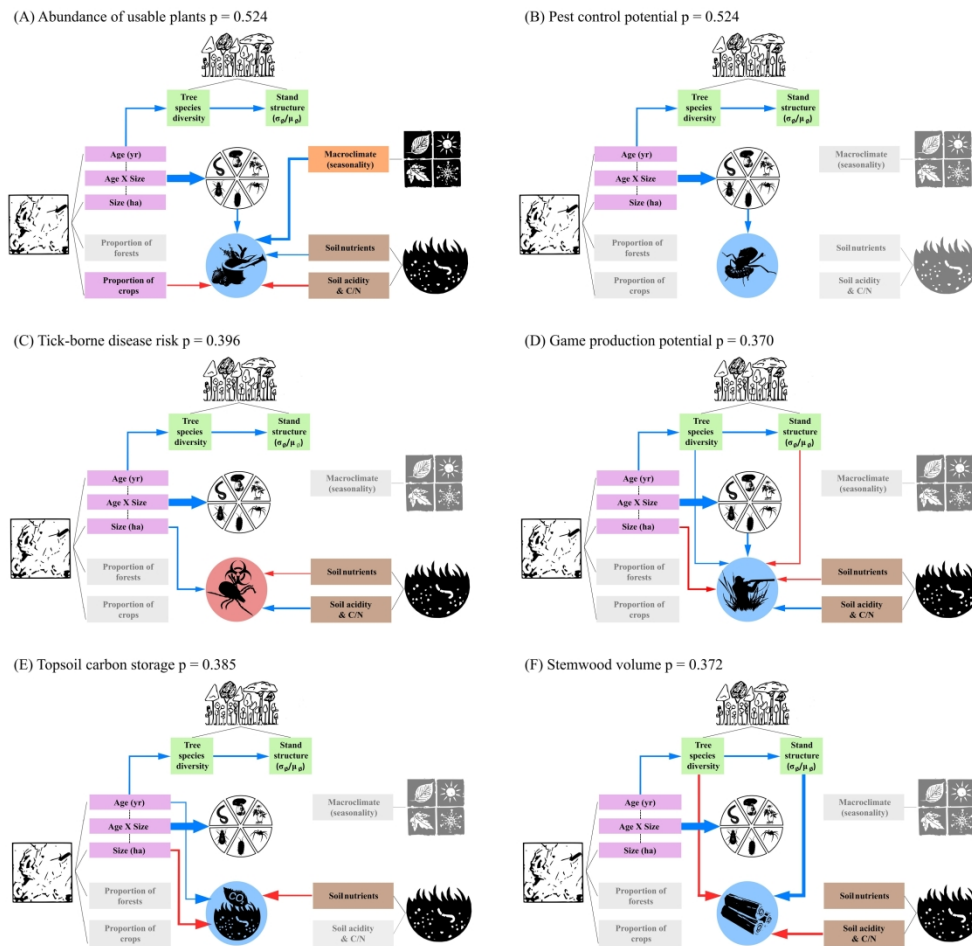


Figure 4: Linkage between the environment, biodiversity and individual ecosystem services in small woodlands across Europe. Results of the piecewise structural equation models studying the response of each individual ecosystem service to multidiversity, patch size, historical age and connectivity (proportion of forests and crops in a 500-m surface around each patch), while accounting also for macroclimate, soil and forest structural characteristics as environmental drivers. Blue arrows indicate positive effects and red arrows indicate negative effects. Arrow thickness is proportional to the effect size. Only significant paths ( $p < 0.05$ ) are shown, while variables not significantly contributing to the models are attenuated and represented with grey shading. The overall p-value for each piecewise structural equation model (piecewise SEM) is shown in the heading of each panel.

294x281mm (300 x 300 DPI)

1 **Supplementary Information**

2 This file contains Appendix S1, Figures S1 to S3 and Tables S1 to S5.

### 3 **Appendix S1: Supplementary Methods.**

#### 4 ***Details on patch selection***

5 We wanted the subset of patches selected for sampling to be representative of  
6 the variation of patch size and historical age within each window. For that  
7 purpose, we divided all patches occurring within a given landscape window into  
8 two categories of size (small vs. large patches) and historical age (historically  
9 old vs. historically young patches), by using the median values of, respectively,  
10 patch size and historical age as division points between categories. Next, we  
11 selected 16 patches per window (i.e., 224 patches in total). Our aim was to  
12 select four patches for each of the combinations of size times historical age  
13 categories (small-old, small-young, large-old, large-young), although due to  
14 various reasons (e.g. some patches being unsuitable for sampling) this was not  
15 always possible. Summary statistics for each category per landscape window  
16 are shown in Table S1).

#### 17 ***Details on soil sampling***

18 Soil samples were taken during the period from August to October 2012 before  
19 leaves were shed and when the soil was well moisturized. For each patch, we  
20 sampled soil evenly along parallel transect lines located 50-m apart from each  
21 other. In the smallest patches (less than 7000 m<sup>2</sup>) a total of 3-5 soil samples  
22 were sampled and subsequently pooled. In bigger patches, the number of soil  
23 samples were related to patch size, ranging from 5 to 31 soil samples per patch  
24 (mean $\pm$ SE = 5.99 $\pm$ 0.26 samples per patch). We used a frame of 25  $\times$  25 cm<sup>2</sup> to  
25 collect forest floor samples. Care was taken not to mix forest floor with mineral  
26 soil when collecting the samples. The mineral soil was sampled using a metal  
27 soil core with a diameter of 4.2 cm. One core sample was taken down to 10 cm  
28 in mineral soil at all places where forest floor was removed. A total of 1315  
29 forest floor samples and 1315 mineral soil samples were taken.

30 The samples were dried at 40°C and subsequently weighed. Ten percent  
31 of the samples were later dried at 105°C to establish a correction factor for  
32 weight loss. The soil was passed through a 1 mm sieve to remove stones and  
33 gravel. Fine and coarse roots were removed by hand and weighed. All samples  
34 were analyzed for pH, total carbon (C) and nitrogen (N) as well as total

35 phosphorous (P) in a single laboratory provider. Soil pH (CaCl<sub>2</sub>) was measured  
36 using a glass electrode (Orion, Orion Europe, Cambridge, England, model  
37 920A) following the procedure described in ISO 10390:1994(E). The  
38 concentration of C and N was measured by high temperature combustion at  
39 1150°C using an elemental analyzer (Vario MACRO cube CNS, Elementar,  
40 Germany). Total P concentration was measured after complete destruction with  
41 HClO<sub>4</sub> (65%), HNO<sub>3</sub> (70%) and H<sub>2</sub>SO<sub>4</sub> (98%) in Teflon bombs for 4 hours at  
42 150°C. P concentrations were measured according to the malachite green procedure  
43 (Lajtha, Driscoll, Jarrell, & Elliott, 1999).

44 For each sample, we calculated the average depth of the forest floor (cm), and  
45 the total C and N contents (Mg ha<sup>-1</sup>), the C:N ratio, the total P content (kg ha<sup>-1</sup>)  
46 and the pH (CaCl<sub>2</sub>) of the mineral topsoil (0-10 cm).

#### 47 ***Details on data collection for forest structural drivers***

48 Data were collected at 1-9 randomly chosen points per patch (number of points  
49 depending on patch size, mean±SE = 2.34±0.13) using an adaptation of the Point-  
50 Center-Quarter (Cottam & Curtis, 1956) method. Instead of one tree per quarter, two  
51 trees per quarter were measured, to gain an increased degree of detail per sample point.  
52 Trees were chosen to be of small and large diameter per quadrant and would thus  
53 represent different layers/historical age classes of the sampled forest patches. Small

54 trees were chosen to be between 7 cm and 30 cm in diameter at breast height (d130) and  
55 larger trees were chosen to be larger than 30 cm at d130. For each tree we recorded the  
56 species, tree height, number of stems, d130, the distance and angle to the central  
57 sampling point and whether the tree was alive. Sampling was restricted to a 20-m radius  
58 around the central point and if no tree of either group was found per quadrant, this was  
59 recorded.

#### 60 ***Details on data collection for biodiversity***

##### 61 *Understory herbs*

62 All patches were comprehensively surveyed for all understory herb (i.e. non-woody)  
63 species by walking along parallel transects located 10-m apart from each other. Along  
64 these transects, we recorded all species seen and thus obtained a quasi-exhaustive value  
65 of understory herb species richness for each patch.

##### 66 *Arthropods*

67 Species richness of arthropods belonging to four taxonomic groups, including ground  
68 beetles (Insecta), spiders (Arachnida), millipedes (Myriapoda) and woodlice (Crustacea)  
69 was evaluated using pitfall trap sampling. We used pitfall traps with a diameter of 10  
70 cm and a depth of 11 cm. Traps were filled with 200 ml of ethylene glycol and water  
71 (1:1). A drop of detergent was added to remove water surface tension and the traps were  
72 equipped with aluminum roofs. In order to sample as much of the whole species  
73 community a sample point was set-up in the center of each patch and a second one was  
74 placed at the south-facing edge of the patch. If the south-facing edge was not suitable  
75 e.g. bordered by a ditch, road or other physical barrier (38 % of the edges), we used the  
76 eastern (16 % of the edges), western (18 %) or northern edge (4 %) instead. Each  
77 sample point consisted of two subsample units spaced five meters from each other. Each

78 subsample unit consisted of two pitfall traps each separated by a plastic barrier (100 cm  
79 × 30 cm), parallel to the forest edge. This setup was used originally to identify species  
80 fluxes. Thus in each forest patch, eight pitfall traps were set up (four in the core and  
81 four at the southern edge). Arthropods were collected twice between April and August  
82 2013. To make data comparable among regions, the two field sampling campaigns  
83 started at Growing Degree Hours values of ca. 10,000 and 20,000 (based on data of  
84 local weather stations in 2008 and 2009), respectively. Traps were open for 14  
85 consecutive days, after which the trap content was collected and transported to the lab  
86 for sorting and subsequent identification. All individuals were identified to the species  
87 level.

### 88 *Mushrooms*

89 In each patch, mushroom species richness was evaluated by recording the presence of  
90 all fruiting bodies encountered along a 6-m wide strip-transect disposed along the  
91 widest diameter of the patch. Under the general name “mushrooms”, we considered  
92 only those fungus producing fruiting bodies (i.e. epigeous sporocarps). Mushroom  
93 sampling was performed in autumn 2013, and in order to standardize the sampling  
94 timing we used six mushroom species with a wide European distribution as  
95 phenological indicators: mushroom sampling started as soon as the sporocarps of one of  
96 the following taxa were observed: *Armillaria* sp.; *Collybia butyracea*; *C. dryophila*;  
97 *Hypholoma fasciculare*; *Laccaria amethystina*; or *Lactarius quietus*. These species  
98 frequently occur during the peak of sporocarp production of most species which  
99 coincides with a peak in autumn rainfall (Bonet et al., 2008). Local and European  
100 encyclopedias and guides (Bon, 2012; Courtecuisse & Duhem, 2013; Eyssartier &  
101 Roux, 2013) as well as databases (Société Mycologique du Nord de la France;  
102 <http://www.smnf.fr/>) were used to identify mushroom species in the field. When the

103 species could not be identified in the field, pictures of the whole sporocarps and, when  
104 possible, details of the cap, pores, stipe, ring, and gill were taken with a digital camera  
105 for species identification.

#### 106 ***Details on data collection for proxies for ecosystem services***

##### 107 *Abundance of usable plants*

108 We performed a second, more detailed vegetation sampling in each patch, where we  
109 walked along parallel transects located 50-m apart from each other and established  
110 sampling plots every 100 m along a given transect. Number of sampling plots per patch  
111 ranged from 1 (for patches smaller than 0.5 ha) to 128 (mean $\pm$ SE = 5 $\pm$ 0.41). We  
112 recorded all vascular species present in the understory within a 10-m radius sampling  
113 plot and their abundance in an ordinal scale (1 = rare, 2 = common, 3 = dominant); i.e. a  
114 simplified version of the Tansley-scale (Tansley, 1935). We used several bibliographic  
115 sources to determine if each of the herbaceous species was of potential use by humans  
116 (see usable species list and references in Table S3). We then summed the abundances of  
117 usable species for each sampling plot, and calculated the average abundance of usable  
118 plants per patch by averaging among all sampling plots within each patch. Note that this  
119 variable is completely independent from the variable measuring understory plant  
120 diversity, which was obtained from a different survey at a different spatial resolution,  
121 i.e. abundance of usable plants was recorded at the plot level whereas understory plant  
122 diversity was recorded at the patch level.

##### 123 *Game production potential*

124 Game production potential was assumed to be correlated with the abundance of  
125 palatable plants for large herbivores (Gamfeldt et al., 2013) and thus calculated as the  
126 average abundance per patch (calculated in a similar way as for usable plants) of the

127 species eaten by roe deer (considering all vascular species, including herbs, shrubs and  
128 trees). We checked bibliography on roe deer diet across Europe and selected the  
129 vascular plant species (or genus) cited in at least three publications (see species list and  
130 references in Table S4). Roe deer was selected since this is an important game species  
131 that occurs in all our study regions, which is not the case for, e.g. red deer or wild boar.  
132 Roe deer needs woody plant species in its diet (Lovari et al., 2017) and thus requires  
133 woodlands or hedgerows within its foraging range. Although there is no direct evidence  
134 in the scientific literature to support our hypothesis that roe deer density is positively  
135 related to the abundance of palatable plant, we argue that such a positive relationship is  
136 very likely and that our approach of using palatable plants as a proxy for game  
137 production potential is robust. Indeed, during the hunting season (mostly autumn and  
138 winter), when food has become rare for roe deer, both in croplands (harvests are  
139 completed and winter wheat has not emerged yet) and grasslands (cattle are still grazing  
140 in the meadows at that time of year), roe deer concentrate in woodlands where most of  
141 the palatable woody plants for roe deer are still available. Besides, roe deer use  
142 woodlands as a shelter against hunters during the hunting season in open farmlands  
143 (which starts before the hunting season in woodlands). This increases the probability for  
144 roe deer diet to solely rely on woody palatable plants from woodland habitats. Besides,  
145 we are not interested in assessing the density of roe deer *per se* here but rather the  
146 potential of a given woodland to provide hunting recreational activities and thus game  
147 production potential should be seen here as a recreational service rather than as a pure  
148 provisioning service for food supply.

#### 149 *Pest control potential*

150 Pest control potential was assessed by the total abundance of malacophagous carabid  
151 beetles per patch from trapping data (see above and Table S5 for the list of

152 malacophagous species and references). The rationale is that the selected  
153 malacophagous carabid beetles will prey on slugs in the adjacent fields; i.e. they use the  
154 forest patches for overwintering and refuge against agricultural disturbances and  
155 migrate to the agricultural land to prey (see references in Table S5). Note that  
156 abundance values from a very restricted set of species (malacophagous beetles) were  
157 used here to compute pest control potential whereas the variable measuring arthropod  
158 diversity is based on occurrence data across four different arthropod groups.

#### 159 *Tick-borne disease risk*

160 Tick-borne disease risk (a disservice) was assumed to be correlated with tick density  
161 because a higher tick density would result in a higher risk for humans to be infected by  
162 tick-borne diseases such as Lyme Borreliosis. For each patch, tick density (i.e. mean  
163 density of nymphs per 100 m<sup>2</sup>) was assessed using a standardized sampling protocol.  
164 All ticks stages were collected via drag sampling (Tack et al., 2011) with a 1 × 1 m<sup>2</sup>  
165 piece of white flannel fabric attached to a wooden pole on a 100-m long transect  
166 (resulting in a 100 m<sup>2</sup> sampled area). Ticks were collected in the close vicinity (less than  
167 25 m distance) of the central sampling point used for forest structure (see above). Ticks  
168 were picked off the cloth after 25 m of dragging and preserved in ethanol before being  
169 identified at the species level and counted in the lab (Ehrmann et al., 2017).

#### 170 *Stemwood volume*

171 Stemwood volume (m<sup>3</sup>) was determined from published species- and region-specific  
172 allometric equations based on tree height and diameter at breast height (d130)  
173 measurements. Species-specific equations to calculate stemwood volume are not  
174 available for all regions, and some species found in forests are not represented by any  
175 equation in the literature. Thus, either generalized regional equations (regional *Quercus*

176 equation for all *Quercus* trees in that region, irrespective of species), generalized  
177 equations irrespective of the region, equations from substitute species (*Quercus robur*  
178 for *Castanea sativa*) or generic equations based merely on d130 and tree height, if no  
179 equations were available for the respective species (Deleuze et al., 2014), were used in  
180 order to calculate stemwood volume (see <https://github.com/EhrmannS/tree-allometry>  
181 for a detailed description of the selection of utilized equations).

#### 182 *Topsoil carbon storage*

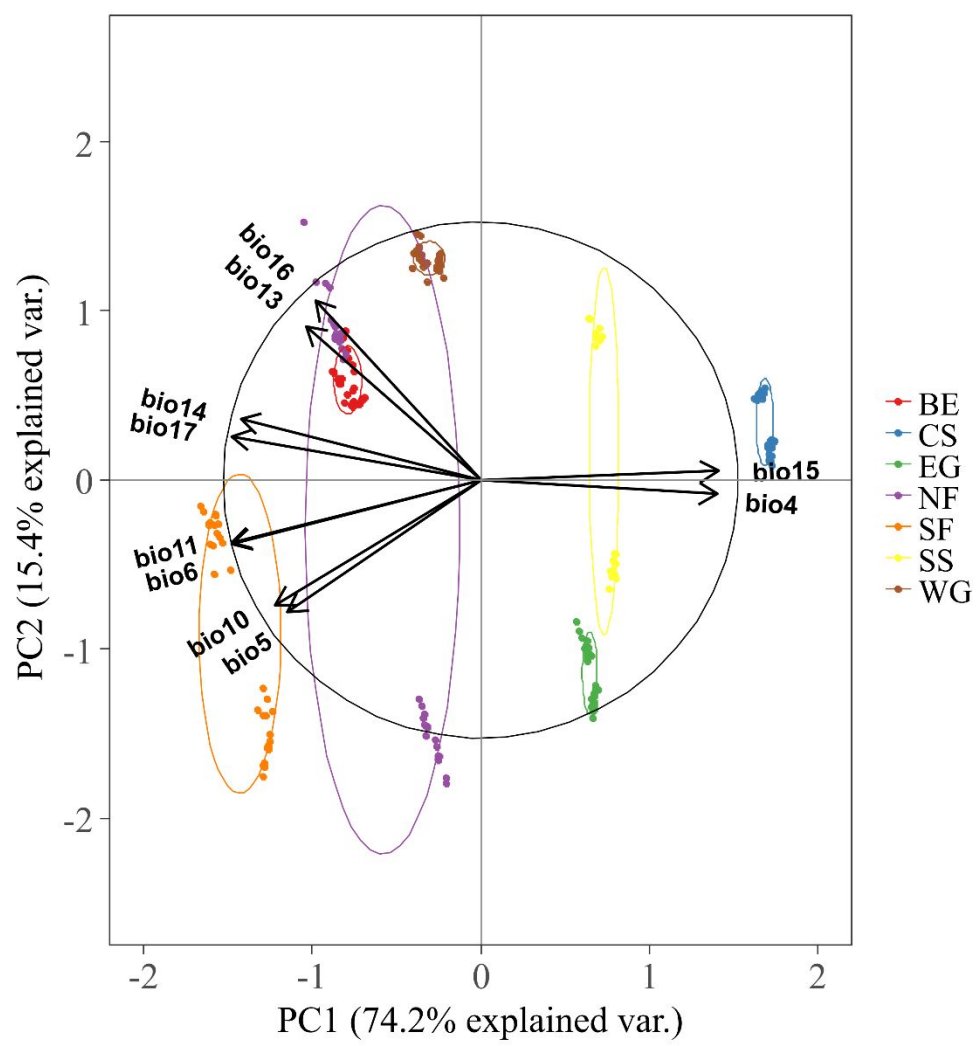
183 We used the soil C content (Mg/ha) in the combined forest floor and mineral topsoil (10  
184 cm) for each patch as a measure of the potential for topsoil carbon storage.

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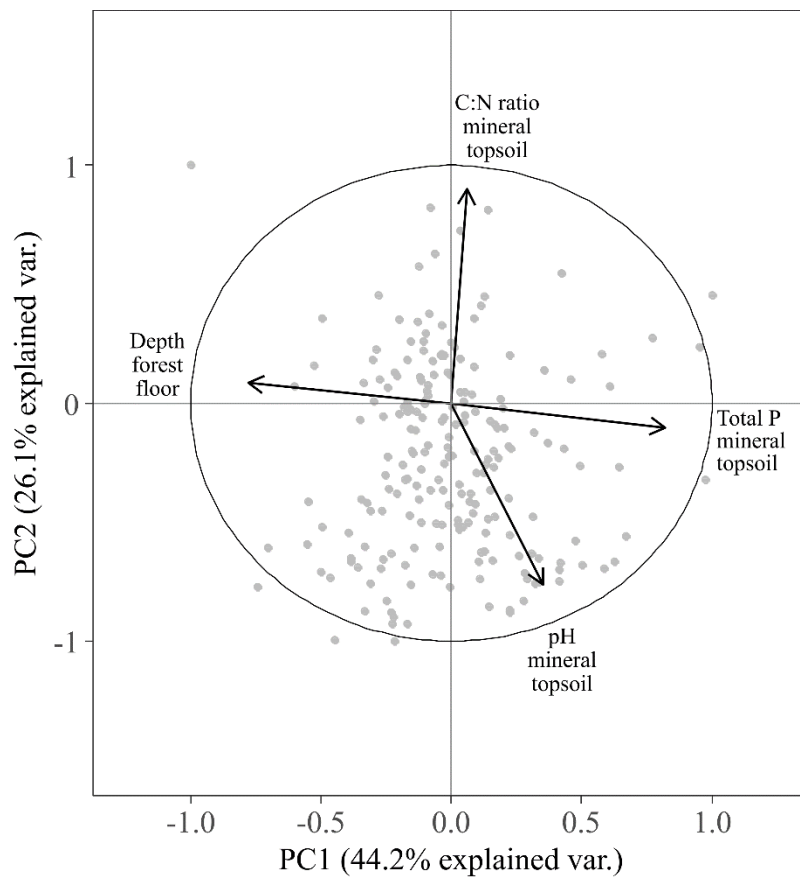
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219 **Figure S1:** Diagram of the principal component analysis (PCA) used to calculate the  
220 variable “macroclimate”. The PCA included 5 temperature variables (BIO4 =  
221 temperature seasonality, BIO5 = maximum temperature of warmest month, BIO6 =  
222 minimum temperature of coldest month, BIO10 = mean temperature of warmest quarter,  
223 BIO11 = mean temperature of coldest quarter) and 5 precipitation variables (BIO15 =  
224 precipitation seasonality, BIO13 = precipitation of wettest month, BIO14 =  
225 precipitation of driest month, BIO16 = precipitation of wettest quarter, BIO17 =  
226 precipitation of driest quarter). The correlation of each variable with the two first  
227 PCA axes is shown. The black circle represents correlation = 1. Points  
228 correspond to observations (patches) classified by region (SF = South France,  
229 NF = North France, BE = Belgium, WG = West Germany, EG = East Germany,  
230 SS = South Sweden, CS = Central Sweden). Colored ellipses include 68% of  
231 the patches in each region.



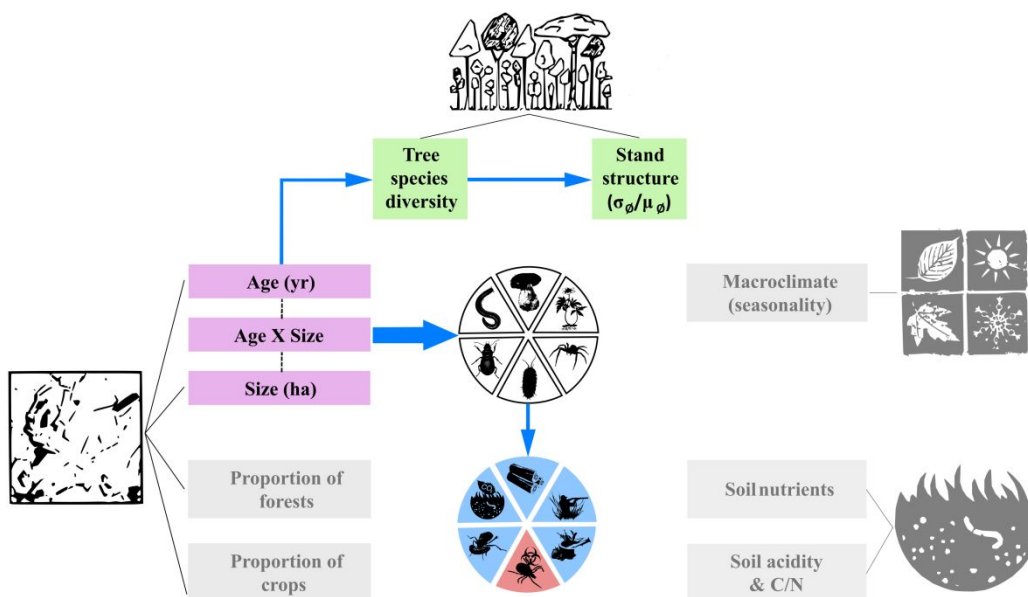
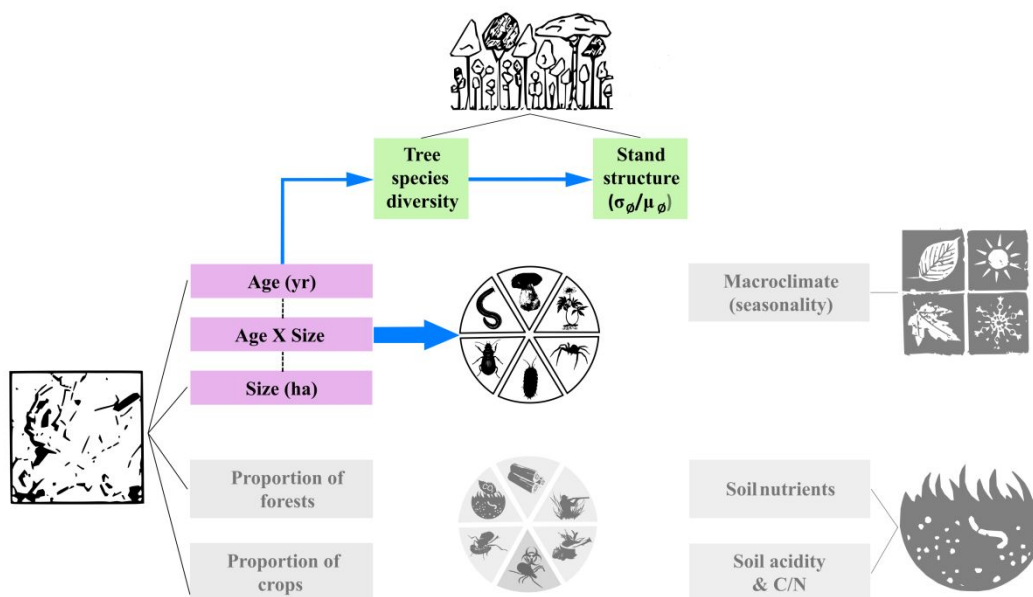
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233 **Figure S2:** Diagram of the principal component analysis (PCA) used to calculate  
234 the variables “soil nutrients” (PCA axis 1) and “soil acidity & C/N” (PCA axis 2).  
235 The PCA included 4 variables: depth of the forest floor and C:N ratio, total P  
236 content and pH of the mineral topsoil. The correlation of each variable with the



237 two first PCA axes is shown. The black circle represents correlation = 1. Points  
238 correspond to observations (patches).

239 **Figure S3:** Linkage between the environment, biodiversity and multiservice delivery  
240 potential in small woodlands across Europe. Results of the piecewise structural equation  
241 models (piecewise SEMs) studying the response of low- (A) and intermediate-  
242 performance (B) multiservice (MS) delivery potential to multidiversity, patch size, age  
243 and connectivity (proportion of forests and crops in a 500-m surface around each patch),  
244 while accounting for macroclimate, soil and forest structural characteristics as  
245 environmental drivers. The variables “region” and “window type” nested within  
246 “region” were included as random effect terms in all component models. Blue arrows  
247 indicate positive effects and red arrows indicate negative effects. Arrow thickness is  
248 proportional to the effect size. Only significant effects ( $p < 0.05$ ) are shown, while  
249 variables not significantly contributing to the models are attenuated and represented  
250 with grey shading. According to Fisher’s C statistic, both SEMs provided an adequate  
251 fit to the data with all p-values all above the 0.05 threshold. The p-value for the global  
252 model is shown in each case.

(A) Low-performance MS delivery potential  $p = 0.477$ (B) Intermediate-performance MS delivery potential  $p = 0.373$ 

254 **Table S1:** Summary statistics for each patch size and age category per landscape  
 255 window. Means and standard deviations (SD) of size and age of the patches are shown,  
 256 as well as the number of patches included in each category (N).

Landscape window	Size category	Age category	N	Size (ha)		Age (years)	
				Mean	SD	Mean	SD
Be_B	large	old	4	11.19	4.46	131.88	22.9
	large	recent	4	2.45	1.58	20.79	15.11
	small	old	4	0.61	0.27	110.45	21.15
	small	recent	4	0.82	0.5	21.04	18.07
Be_O	large	old	4	9.21	2.77	210.25	12.4
	large	recent	4	2.25	1.65	51.33	45.96
	small	old	4	0.58	0.4	212.73	33.67
	small	recent	4	0.44	0.16	54.26	48.9
Fr_N_B	large	old	4	9.54	12.04	79.36	42.32
	large	recent	4	1.59	0.54	24.6	9.04
	small	old	4	0.59	0.26	50.84	8.75
	small	recent	4	0.38	0.28	12	0
Fr_N_O	large	old	4	12.62	10.3	133.47	20.66
	large	recent	4	3.06	1.02	43.82	21.32
	small	old	4	1.28	0.65	90.76	19.48
	small	recent	4	0.66	0.58	39.02	18.83
Fr_S_B	large	old	4	4.05	2.35	91.91	34.87
	large	recent	4	4.88	3.07	31.69	16.34
	small	old	4	0.53	0.21	44.74	4.59


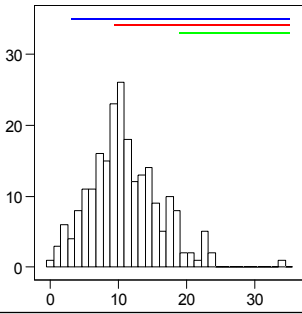

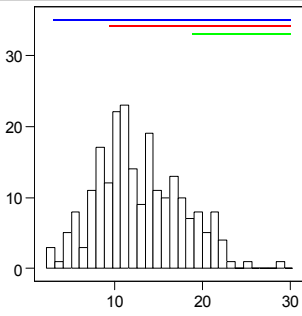

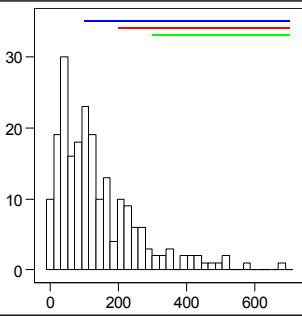

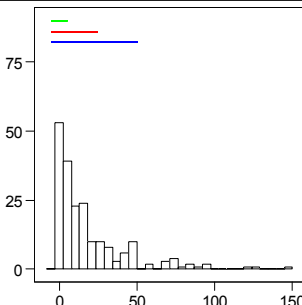
	small	recent	4	0.41	0.17	17.16	10.32
Fr_S_O	large	old	5	9.04	2.99	125.44	6.4
	large	recent	3	4.27	1.66	12	0
	small	old	4	1.18	0.48	88.86	50.69
	small	recent	4	0.55	0.18	12	0
Ge_E_B	large	old	8	5.8	3.42	122.27	69
	large	recent	0	-	-	-	-
	small	old	1	2.48	-	70.51	-
	small	recent	7	1.14	0.39	12	0
Ge_E_O	large	old	7	21.4	17.71	136.03	38.75
	large	recent	2	2.87	1.03	57.65	48.49
	small	old	2	2.05	0.4	119.32	41.59
	small	recent	7	0.89	0.35	21.82	25.97
Ge_W_B	large	old	4	7.2	5.14	107.17	50.09
	large	recent	4	2.34	0.57	12	0
	small	old	4	0.72	0.44	115.08	90.8
	small	recent	4	0.37	0.13	12	0
Ge_W_O	large	old	4	7.2	6.53	139.73	39.46
	large	recent	1	1.82	-	37.29	-
	small	old	4	0.82	0.36	101.21	42.35
	small	recent	7	0.73	0.47	22.31	14.34
Sw_C_B	large	old	4	0.94	0.7	90.91	76.82
	large	recent	4	1.08	0.26	13.11	2.21
	small	old	4	0.28	0.06	87.53	43.11
	small	recent	4	0.18	0.1	12	0

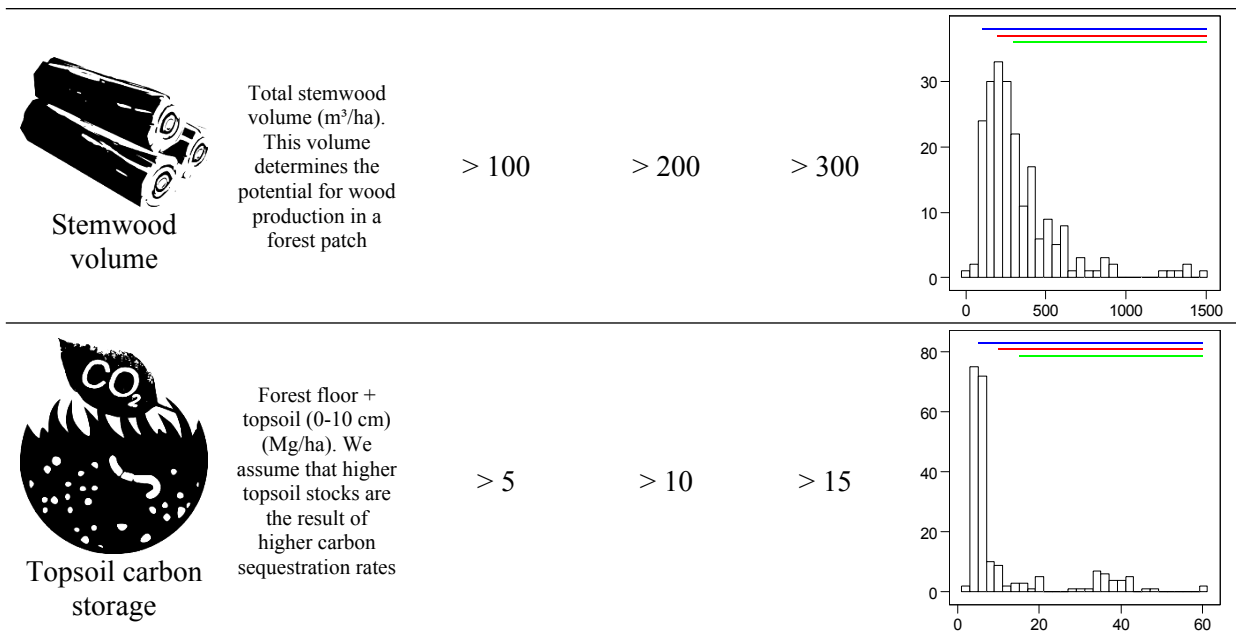
Sw_C_O	large	old	4	2.74	1.84	125.85	95.19
	large	recent	4	4.78	5.79	12	0
	small	old	4	0.62	0.2	48.09	14.82
	small	recent	4	0.64	0.19	17.08	10.17
Sw_S_B	large	old	10	9.48	10.32	202.9	53
	large	recent	2	2.14	0	57.98	65.02
	small	old	1	0.38	-	107.6	-
	small	recent	3	0.86	0.33	35.04	18.31
Sw_S_O	large	old	7	8.85	8.08	90.5	45.22
	large	recent	2	7.01	6.47	24.46	17.62
	small	old	1	2.2	-	235.42	-
	small	recent	6	1.08	0.46	23.59	18.19

258 **Table S2:** Details on the definition of thresholds of low, intermediate and high  
259 performance levels of multiservice delivery for each individual ecosystem  
260 service proxy. The blue, red, and green lines above the histograms entail  
261 patches with low, intermediate, and high performance levels, respectively.

262 Abundances of usable plants and game production potential were calculated as  
263 averages of abundances among all sampling plots within each patch. Each  
264 sampling plot was a circle of 10-m radius (314 m<sup>2</sup>) where abundances of  
265 individual species were recorded in an ordinal scale (1 = rare, 2 = common, 3 =  
266 dominant; i.e. a simplified version of the Tansley-scale (Tansley, 1935)) and  
267 summed. For these two ecosystem services we have chosen threshold values  
268 that represent different abundances per 100 m<sup>2</sup>. In general, the threshold  
269 values aimed to reflect tangible values that are meaningful for practitioners, and  
270 were determined after consultation of the literature for pest control potential  
271 (Rouabah, Villerd, Amiaud, Plantureux, & Lasserre-Joulin, 2015), tick-borne  
272 disease risk (Ruyts et al., 2018), stemwood volume (FAO, 2015a, 2015b) and  
273 topsoil carbon storage (Vesterdal, Schmidt, Callesen, Nilsson, & Gundersen,  
274 2008). The thresholds for the abundance of usable plants and the game

- 275 production potential were based on expert judgment by the paper's core author
- 276 team (AV, JL, PDF, KV, and GD) since literature data were lacking.

Ecosystem service proxy	Units	Threshold values			Histogram
		Low	Medium	High	
 Abundance of usable plants	Mean total cover in a 10 m radius plot (314 m <sup>2</sup> ). Cover scale: 1 rare; 2 common; 3 dominant. Usable plants are defined in Table S3. The more abundant they are, the higher the production	> 1 rare species per 100 m <sup>2</sup> (i.e. value of 3.14)	> 1 dominant species per 100 m <sup>2</sup> (i.e. 9.42)	> 2 dominant species per 100 m <sup>2</sup> (i.e. 18.84)	
 Game production potential	For the game production potential we assumed that a high abundance of plants palatable for roe deer (see Table S4) is positively linked to the abundance of roe deer; an important game species in the studied landscapes	> 1 rare species per 100 m <sup>2</sup> (i.e. value of 3.14)	> 1 dominant species per 100 m <sup>2</sup> (i.e. 9.42)	> 2 dominant species per 100 m <sup>2</sup> (i.e. 18.84)	
 Pest control potential	Number of slug-eating carabids found in 8 pitfall traps during two trapping periods. We assume that a high carabid abundance will decrease slug abundance (thus increasing the pest control potential)	> 100	> 200	> 300	
 Tick-borne disease risk	Mean nymphs density per 100 m <sup>2</sup> . Density of nymphs determines the density of Borrelia-infected nymphs, which is a key proxy for disease risk	< 50	< 25	< 5	



277

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299 **Table S3:** List of understory forest herb species present in the sampled forest patches  
 300 and considered to be of potential use for humans. We used several bibliographic sources  
 301 (Couplan, 2009; Ducerf, 2013; Mabey & Blamey, 1989; Mears & Hillman, 2007;  
 302 Toby, Denham, & Whitelegg, 2016) to determine if each of the understory herb  
 303 species found in the vegetation surveys was of potential use by humans. We used  
 304 Couplan (2009) as the primary source, as it was the most complete, providing detailed  
 305 indications on plant uses. Uses were divided in 3 categories: food use, medicinal use  
 306 and other uses. Plant use was only considered when used in Europe (from France to  
 307 Scandinavia, from the United Kingdom to Poland). Supposed or potential uses were not  
 308 considered and only realized uses were considered. Plants that are used but which are  
 309 not forest or forest edge species have not been considered, as forest populations of these  
 310 species will never be used because there are much larger populations outside forests  
 311 (e.g. *Papaver rhoeas*, *Hypochoeris radicata*, *Chenopodium album*, *Lamium album*,  
 312 *Plantago* spp., etc.).

Species name	Food	Medicinal	Other
<i>Adoxa moschatellina</i>	X	X	
<i>Aegopodium podagraria</i>	X	X	
<i>Agrimonia eupatoria</i>	X	X	X
<i>Ajuga reptans</i>	X	X	
<i>Alliaria petiolata</i>	X	X	
<i>Allium oleraceum</i>	X		
<i>Allium schoenoprasum</i>	X		
<i>Allium scorodoprasum</i>	X		
<i>Allium ursinum</i>	X		
<i>Allium vineale</i>	X		
<i>Anacamptis morio</i>	X	X	
<i>Anacamptis pyramidalis</i>	X		
<i>Angelica sylvestris</i>	X	X	
<i>Anthemis tinctoria</i>		X	
<i>Anthoxanthum odoratum</i>	X	X	
<i>Anthriscus caucalis</i>	X		
<i>Anthriscus sylvestris</i>	X		
<i>Aquilegia vulgaris</i>	X		X
<i>Arctium lappa</i>	X	X	

<i>Arctium minus</i>	X	X	
<i>Arctium tomentosum</i>	X	X	
<i>Arrhenatherum elatius ssp. bulbosum</i>	X		
<i>Arum italicum</i>	X	X	
<i>Arum maculatum</i>	X	X	
<i>Arum sp.</i>	X	X	
<i>Asphodelus albus</i>	X		X
<i>Asplenium trichomanes</i>		X	
<i>Bryonia dioica</i>	X	X	
<i>Calla palustris</i>	X		
<i>Campanula trachelium</i>	X		
<i>Cardamine amara</i>	X		
<i>Cardamine flexuosa</i>	X		
<i>Cardamine impatiens</i>	X		
<i>Cardamine pratensis</i>	X	X	
<i>Centaureum erythraea</i>	X		
<i>Cerastium semidecandrum</i>	X		
<i>Chrysosplenium alternifolium</i>	X		
<i>Chrysosplenium oppositifolium</i>	X		
<i>Cirsium oleraceum</i>	X		
<i>Cirsium palustre</i>	X		
<i>Cistus salviifolius</i>	X		
<i>Clinopodium sp.</i>		X	
<i>Clinopodium vulgare (Satureja vulgaris)</i>	X		
<i>Conopodium majus</i>	X		
<i>Dactylis glomerata</i>	X		
<i>Dactylorhiza maculata</i>	X		
<i>Deschampsia cespitosa</i>	X		
<i>Deschampsia flexuosa (Avenella flexuosa)</i>	X		
<i>Dipsacus fullonum</i>	X		
<i>Dryopteris filix-mas</i>	X	X	
<i>Elytrigia repens (Elymus repens)</i>	X	X	
<i>Epilobium angustifolium</i>	X		
<i>Epilobium montanum</i>	X	X	
<i>Epilobium palustre</i>	X		
<i>Epilobium parviflorum</i>	X	X	
<i>Epilobium tetragonum</i>	X		
<i>Equisetum arvense</i>	X	X	X
<i>Equisetum fluviatile</i>	X	X	X
<i>Equisetum hyemale</i>	X	X	X
<i>Equisetum palustre</i>	X	X	X
<i>Equisetum pratense</i>		X	X
<i>Equisetum ramosissimum</i>		X	X
<i>Equisetum sp.</i>		X	X
<i>Equisetum sylvaticum</i>	X	X	X
<i>Equisetum telmateia</i>	X	X	X

<i>Euphorbia amygdaloides</i>			X
<i>Euphorbia dulcis</i>			X
<i>Euphorbia cyparissias</i>			X
<i>Filipendula ulmaria</i>	X	X	X
<i>Fragaria moschata</i>	X		
<i>Fragaria vesca</i>	X	X	
<i>Galanthus nivalis</i>	X		X
<i>Galeopsis bifida_tetrahit</i>	X		
<i>Galium aparine</i>	X		
<i>Galium odoratum (Asperula odorata)</i>	X	X	X
<i>Galium verum</i>	X		X
<i>Genista tinctoria</i>	X	X	X
<i>Geum rivale</i>	X	X	
<i>Geum urbanum</i>	X	X	
<i>Glechoma hederacea</i>	X	X	
<i>Glyceria fluitans</i>	X		
<i>Heracleum sphondylium</i>	X	X	
<i>Humulus lupulus</i>	X	X	X
<i>Hyacinthoides non-scripta</i>			X
<i>Hypericum perforatum</i>	X	X	X
<i>Hypericum tetrapterum (Hypericum quadrangulum)</i>	X		
<i>Lamium galeobdolon (Galeobdolon luteum)</i>	X		
<i>Lamium maculatum</i>	X		
<i>Lapsana communis</i>	X	X	
<i>Lathyrus linifolius</i>	X		
<i>Lathyrus linifolius var. montanus</i>	X		
<i>Lathyrus sylvestris</i>	X		
<i>Leucojum vernum</i>			X
<i>Lunaria rediviva</i>			X
<i>Lythrum portula (Peplis portula)</i>	X	X	
<i>Lythrum salicaria</i>	X		
<i>Maianthemum bifolium</i>	X		
<i>Mentha aquatica</i>	X		
<i>Milium effusum</i>	X		
<i>Moehringia trinervia</i>	X		
<i>Monotropa hypopitys</i>	X	X	
<i>Mycelis muralis (Lactuca muralis)</i>	X		
<i>Nasturtium officinale</i>	X	X	
<i>Orchis mascula</i>	X	X	
<i>Orchis purpurea</i>	X	X	
<i>Origanum vulgare</i>	X	X	
<i>Ornithogalum pyrenaicum</i>	X		
<i>Ornithogalum umbellatum</i>	X		X
<i>Oxalis acetosella</i>	X	X	
<i>Phyteuma nigrum</i>	X		
<i>Phyteuma spicatum</i>	X		

<i>Picris echioides</i>	X		
<i>Picris hieracioides</i>	X		
<i>Platanthera bifolia</i>	X	X	
<i>Polygonatum multiflorum</i>	X		
<i>Polygonatum odoratum</i>	X	X	
<i>Polygonum amphibium</i>	X		
<i>Polygonum bistorta</i>	X		
<i>Polypodium vulgare</i>	X		
<i>Potentilla erecta</i>		X	
<i>Primula elatior</i>	X	X	
<i>Primula veris</i>	X	X	
<i>Primula vulgaris</i>	X	X	
<i>Prunella vulgaris</i>	X	X	
<i>Pteridium aquilinum</i>	X		X
<i>Pulmonaria obscura</i>	X		
<i>Pulmonaria officinalis</i>	X	X	
<i>Rubia peregrina</i>	X		X
<i>Rumex obtusifolius</i>	X	X	
<i>Rumex sanguineus</i>	X	X	
<i>Ruscus aculeatus</i>	X	X	X
<i>Sambucus ebulus</i>			X
<i>Sanicula europaea</i>		X	
<i>Scirpus sylvaticus</i>	X		
<i>Scrophularia nodosa</i>		X	
<i>Sedum telephium</i>	X		X
<i>Sedum telephium subsp. maximum</i>	X		X
<i>Senecio viscosus</i>		X	
<i>Silene vulgaris</i>	X		X
<i>Solanum dulcamara</i>			X
<i>Solanum nigrum</i>			X
<i>Solidago virgaurea</i>		X	
<i>Spartium junceum</i>		X	
<i>Stachys officinalis</i>		X	
<i>Stachys sylvatica</i>	X	X	
<i>Stellaria alsine (Stellaria uliginosa)</i>	X		
<i>Stellaria media</i>	X	X	
<i>Stellaria nemorum</i>	X	X	
<i>Succisa pratensis</i>		X	
<i>Symphytum officinale</i>	X	X	
<i>Tamus communis</i>	X	X	
<i>Teucrium scorodonia</i>		X	
<i>Thymus serpyllum</i>	X		
<i>Typha angustifolia</i>	X	X	
<i>Typha latifolia</i>	X	X	
<i>Urtica dioica</i>	X	X	X
<i>Vaccinium myrtillus</i>	X	X	

<i>Vaccinium uliginosum</i>	X	X	
<i>Vaccinium vitis-idaea</i>	X	X	
<i>Valeriana officinalis (Valeriana repens)</i>	X	X	
<i>Veronica officinalis</i>	X	X	
<i>Vicia sepium</i>	X		
<i>Viola odorata</i>	X		X
<i>Viola reichenbachiana</i>	X		X
<i>Viola riviniana</i>	X		

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323 **Table S4:** List of species present in the sampled forest patches and considered to be  
 324 palatable for roe deer, i.e. cited in at least three of the references consulted hereafter:  
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 326 Bartolomé, Rosell, & Bassols, 2002; Cederlund & Nyström, 1981; Czernik et al., 2013;  
 327 de Jong, Gill, van Wieren, & Burlton, 1995; Helle, 1980; Henry, 1975; Jackson, 1980;  
 328 Kamler & Homolka, 2005; Maizeret, Boutin, Cibien, & Carlino, 1989; Moser, Schütz,  
 329 & Hindenlang, 2008; Mysterud, Lian, & Hjermann, 1999; Schmidt, Sommer,  
 330 Kriebitzsch, Ellenberg, & Oheimb, 2004; Storms et al., 2008; Tixier et al., 1997; and  
 331 Wallach, Shanas, & Inbar, 2010.

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**Species name**

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*Agrostis canina*

*Agrostis capillaris (Agrostis tenuis)*

*Agrostis gigantea*

*Agrostis sp.*

*Agrostis stolonifera*

*Betula pendula*

*Betula pubescens*

*Calluna vulgaris*

*Carex acuta*

*Carex acutiformis*

*Carex appropinquata*

*Carex brunnescens*

*Carex buxbaumii*

*Carex canescens (Carex curta)*

*Carex cespitosa*

*Carex cuprina*

*Carex demissa (Carex viridula subsp. oedocarpa)*

*Carex diandra*

*Carex digitata*

*Carex divulsa*

*Carex echinata*

*Carex elata*

*Carex elongata*

*Carex flacca*

*Carex flava*

*Carex hirsuta*

*Carex hirta*

*Carex loliacea*

*Carex montana*

*Carex muricata* agg.  
*Carex nigra*  
*Carex ovalis* (*Carex leporina*)  
*Carex pallescens*  
*Carex pendula*  
*Carex pilulifera*  
*Carex pseudobrizoides*  
*Carex pseudocyperus*  
*Carex remota*  
*Carex riparia*  
*Carex rostrata*  
*Carex* sp.  
*Carex spicata* agg.  
*Carex strigosa*  
*Carex sylvatica*  
*Carex umbrosa*  
*Carex vaginata*  
*Carex vesicaria*  
*Carex vulpina*  
*Deschampsia cespitosa*  
*Deschampsia flexuosa* (*Avenella flexuosa*)  
*Fagus sylvatica*  
*Festuca arundinacea*  
*Festuca gigantea*  
*Festuca heterophylla*  
*Festuca ovina* agg.  
*Festuca pratensis*  
*Festuca rubra*  
*Festuca* sp.  
*Hedera helix*  
*Holcus lanatus*  
*Holcus mollis*  
*Luzula campestris*  
*Luzula forsteri*  
*Luzula luzuloides*  
*Luzula multiflora*  
*Luzula pallescens*  
*Luzula pilosa*  
*Luzula* sp.  
*Picea abies*  
*Picea sitchensis*  
*Pinus sylvestris*  
*Poa annua*  
*Poa bulbosa*  
*Poa nemoralis*  
*Poa palustris*

*Poa pratensis*  
*Poa pratensis* ssp. *angustifolia* (*Poa angustifolia*)  
*Poa* sp.  
*Poa trivialis*  
*Populus tremula*  
*Prunus avium*  
*Prunus cerasifera*  
*Prunus cerasifera* f. *atropurpurea*  
*Prunus cerasus*  
*Prunus domestica* ssp. *insititia*  
*Prunus laurocerasus*  
*Prunus mahaleb*  
*Prunus padus* (*Padus avium*)  
*Prunus serotina*  
*Prunus* sp.  
*Prunus spinosa*  
*Quercus ilex*  
*Quercus petraea*  
*Quercus pubescens*  
*Quercus robur*  
*Quercus rubra*  
*Quercus* sp.  
*Rubus caesius*  
*Rubus fruticosus* agg.  
*Rubus idaeus*  
*Rubus saxatilis*  
*Rubus* sp.  
*Rubus spectabilis*  
*Rumex acetosa*  
*Rumex acetosella*  
*Rumex conglomeratus*  
*Rumex crispus*  
*Rumex longifolius*  
*Rumex obtusifolius*  
*Rumex sanguineus*  
*Rumex* sp.  
*Salix alba*  
*Salix aurita*  
*Salix caprea*  
*Salix cinerea*  
*Salix fragilis*  
*Salix pentandra*  
*Salix* sp.  
*Salix triandra*  
*Salix viminalis*  
*Sorbus aucuparia*

*Urtica dioica*

*Vaccinium myrtillus*

*Vaccinium vitis-idaea*

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**Table S5:** List of carabid species present in the sampled forest patches considered as malacophagous according to the references consulted hereafter: Bohan et al., 2000; Brandmayr & Brandmayr, 1986; Cornic, 1973; Dajoz, 2002; Davies, 1953; Dennison & Hodkinson, 1983; Fawki & Toft, 2005; Grimm, Paill, & Kaiser, 2000; Gruntal & Sergeyeva, 1989; Henderson et al., 1996; Holland, 2002; Jelaska, Franjevic, JelASKA, & Symondso, 2014; Kromp, 1999; M. Loreau, 1984; Michel Loreau, 1983; McKemey, Symondson, Glen, & Brain, 2001; Mitchell, 1963; Pakarinen, 1994; Poulin & O’Neil, 1969; Ribera, Foster, Downie, McCracken, & Abernethy, 1999; Scherney, 1960, 2003; Sergeyeva & Gryuntal, 1990; W. O. Symondson, 2004; W. O. C. Symondson, 1989; W. O. C. Symondson, Glen, Wiltshire, Langdon, & Liddell, 1996; W. O. C. Symondson & Liddell, 1993, 1996; Tod, 1973; and Zhavoronkova, 1969.

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**Species name**

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*Abax parallelepipedus*

*Abax parallelus*

*Amara aulica*

*Amara lunicollis*

*Amara similata*

*Anchomenus dorsalis*

*Anisodactylus*

*Anisodactylus binotatus*

*Broscus cephalotes*

*Calathus erratus*

*Calathus fuscipes*

*Calathus luctuosus*

*Calathus melanocephalus*

*Calathus micropterus*

*Calathus rotundicollis*

*Calosoma inquisitor*

*Carabus arvensis*

*Carabus auratus*

*Carabus auronitens*

*Carabus cancellatus*

*Carabus convexus*

*Carabus coriaceus*

*Carabus granulatus*

*Carabus hortensis*

*Carabus monilis*  
*Carabus nemoralis*  
*Carabus problematicus*  
*Carabus violaceus purpurascens*  
*Chlaeniellus nigricornis*  
*Cychrus caraboides*  
*Harpalus latus*  
*Harpalus tardus*  
*Laemonestus terricola*  
*Licinus depressus*  
*Molops piceus*  
*Nebria brevicollis*  
*Nebria salina*  
*Poecilus cupreus*  
*Poecilus lepidus*  
*Poecilus versicolor*  
*Pseudoophonus rufipes*  
*Pterostichus anthracinus*  
*Pterostichus cristatus*  
*Pterostichus kugelannii*  
*Pterostichus macer*  
*Pterostichus madidus*  
*Pterostichus melanarius*  
*Pterostichus niger*  
*Pterostichus nigrata*  
*Pterostichus oblongopunctatus*  
*Semiophonus signaticornis*  
*Trechus gr. Quadristriatus*  
*Trechus secalis*

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