



HAL
open science

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.

► **To cite this version:**

Alicia Valdés, Jonathan Roger Michel Henri Lenoir, Pieter de Frenne, Emilie Andrieu, Jorg Brunet, et al.. High ecosystem service delivery potential of small woodlands in agricultural landscapes. *Journal of Applied Ecology*, 2020, 57 (1), pp.4-16. 10.1111/1365-2664.13537 . hal-02618817

HAL Id: hal-02618817

<https://hal.inrae.fr/hal-02618817>

Submitted on 10 Nov 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 TITLE: “Small but strong: High ecosystem service delivery potential of small woodlands in
2 agricultural landscapes”

3 AUTHOR LIST: Alicia Valdés^{1*}, Jonathan Lenoir^{1*}, Pieter De Frenne^{2*}, Emilie Andrieu³,
4 Jörg Brunet⁴, Olivier Chabrier¹, Sara A. O. Cousins⁵, Marc Deconchat³, Pallieter De Smedt²,
5 Martin Diekmann⁶, Steffen Ehrmann⁷, Emilie Gallet-Moron¹, Stefanie Gärtner⁷, Brice
6 Giffard³, Karin Hansen⁸, Martin Hermy⁹, Annette Kolb⁶, Vincent Le Roux¹, Jaan Liira¹⁰,
7 Jessica Lindgren⁵, Ludmilla Martin¹, Tobias Naaf¹, Taavi Paal¹⁰, Willem Proesmans²,
8 Michael Scherer-Lorenzen⁷, Monika Wulf¹, Kris Verheyen^{2**}, Guillaume Decocq^{1**}.

9 *These authors contributed equally to the work

10 **Shared last authorship

11 †Corresponding author, e-mail: 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 ¹“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, ²Forest &
18 Nature Lab, Ghent University, Geraardsbergsesteenweg 267, B-9090 Melle-Gontrode,
19 Belgium, ³UMR 1201 DYNAFOR, INRA, Chemin de Borde Rouge, CS 52627 F-31326
20 Castanet, France, ⁴Southern Swedish Forest Research Centre, Swedish University of
21 Agricultural Sciences, Box 49, SE-230 53 Alnarp, Sweden, ⁵Landscape Ecology, Department
22 of Geography and Quaternary Geology, Stockholm University, SE-106 91 Stockholm,
23 Sweden, ⁶Vegetation Ecology and Conservation Biology, Institute of Ecology, FB2,
24 University of Bremen, Leobener Strasse, D-28359 Bremen, Germany, ⁷Chair of Geobotany,

25 Faculty of Biology, University of Freiburg, Schaezlestrasse 1, 79104 Freiburg, Germany,
26 ⁸IVL Swedish Environmental Research Institute, Box 210 60, S-100 31 Stockholm, Sweden,
27 ⁹Division Forest, Nature and Landscape Research, University of Leuven (KU Leuven),
28 Celestijnenlaan 200E, B-3000 Leuven, Belgium, ¹⁰Institute of Ecology and Earth Sciences,
29 University of Tartu, Lai 40, EE-51005 Tartu, Estonia, ¹¹Leibniz-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 5×5 km²
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 Valdes 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 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 χ^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, Chabrierie, 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 (Chabrierie, 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
455 publication.

456 ACKNOWLEDGEMENTS

457 We acknowledge Catherine Bataillon, Déborah Closset-Kopp, Katharina Filzen, Kent
458 Hansson, Aurélien Jamoneau, Tom Macheleidt, Willem Proesmans, Laurent Raison, Robert
459 Saguez, Ilka Strubelt, Johan Van Keer, Rieneke Vanhulle, Stephan Wehling, Jérôme Willm
460 and Christina Wolterink for fieldwork, Filip Moldan, Luc Willems, Greet de Bruyn and Lars
461 Rosenqvist for help with soil analyses, Régis Courtecuisse and Pierre-Arthur Moreau for help
462 with mushroom identification, Jérôme Buridant for help with patch history, Justine Louvel for
463 database elaboration, Peter Manning for comments on an earlier version of the manuscript and
464 Margot Vanhellemont for checking the English language. Funding: This research was funded
465 by the ERA-Net BiodivERsA project smallFOREST, with the national funders ANR (France),
466 MINECO (Spain), FORMAS (Sweden), ETAG (Estonia), DFG (Germany), BELSPO
467 (Belgium) and DLR (Germany) part of the 2011 BiodivERsA call for research proposals.

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
471 article.

472 REFERENCES

- Adler, P. B., White, E. P., Lauenroth, W. K., Kaufman, D. M., Rassweiler, A., & Rusak, J. A. (2005). Evidence
for a general species–time–area relationship. *Ecology*, *86*(8), 2032–2039. doi: 10.1890/05-0067
- Allan, E., Bossdorf, O., Dormann, C. F., Prati, D., Gossner, M. M., Tschardtke, T., ... Fischer, M. (2014).
Interannual variation in land-use intensity enhances grassland multidiversity. *Proceedings of the
National Academy of Sciences*, *111*(1), 308–313. doi: 10.1073/pnas.1312213111

- Bagstad, K., Villa, F., Batker, D., Harrison-Cox, J., Voigt, B., & Johnson, G. (2014). From theoretical to actual ecosystem services: mapping beneficiaries and spatial flows in ecosystem service assessments. *Ecology and Society*, *19*(2). doi: 10.5751/ES-06523-190264
- Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D., & Schmid, B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, *9*(10), 1146–1156. doi: 10.1111/j.1461-0248.2006.00963.x
- Balvanera, P., Siddique, I., Dee, L., Paquette, A., Isbell, F., Gonzalez, A., ... Griffin, J.N. (2013). Linking biodiversity and ecosystem services: current uncertainties and the necessary next steps. *BioScience*, *64*(1), 49–57. doi: 10.1093/biosci/bit003
- Bastian., O. (2013). The role of biodiversity in supporting ecosystem services in Natura 2000 sites. *Ecological Indicators*, *24*(1), 12–22. doi: 10.1016/j.ecolind.2012.05.016
- Bodin, Ö., Tengö, M., Norman, A., Lundberg, J., & Elmqvist, T. (2006). The value of small size: loss of forest patches and ecological thresholds in Southern Madagascar. *Ecological Applications*, *16*(2), 440–451. doi: 10.1890/1051-0761(2006)016[0440:TVOSSL]2.0.CO;2
- Byrnes, J. E. K., Gamfeldt, L., Isbell, F., Lefcheck, J. S., Griffin, J. N., Hector, A., ... Emmett Duffy, J. (2014). Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. *Methods in Ecology and Evolution*, *5*(2), 111–124. doi: 10.1111/2041-210X.12143
- Chabrierie, O., Jamoneau, A., Gallet-Moron, E., & Decocq, G. (2013). Maturation of forest edges is constrained by neighbouring agricultural land management. *Journal of Vegetation Science*, *24*(1), 58–69. doi: 10.1111/j.1654-1103.2012.01449.x
- Craven, D., Filotas, E., Angers, V. A., & Messier, C. (2016). Evaluating resilience of tree communities in fragmented landscapes: linking functional response diversity with landscape connectivity. *Diversity and Distributions*, *22*(5), 505–518. doi: 10.1111/ddi.12423
- De Frenne, P., Baeten, L., Graae, B. J., Brunet, J., Wulf, M., Orczewska, A., ... Verheyen, K. (2011). Interregional variation in the floristic recovery of post-agricultural forests. *Journal of Ecology*, *99*(2), 600–609. doi: 10.1111/j.1365-2745.2010.01768.x
- De Frenne, P., Rodríguez-Sánchez, F., Coomes, D. A., Baeten, L., Verstraeten, G., Vellend, M., ... Verheyen, K. (2013). Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences*, *110*(46), 18561–18565. doi: 10.1073/pnas.1311190110

- De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M., ... Lenoir, J. (2019). Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution*, 3(5), 744. doi: 10.1038/s41559-019-0842-1
- Decocq, G., Andrieu, E., Brunet, J., Chabrierie, O., Frenne, P. D., Smedt, P. D., ... Wulf, M. (2016). Ecosystem services from small forest patches in agricultural landscapes. *Current Forestry Reports*, 2(1), 30–44. doi: 10.1007/s40725-016-0028-x
- Donald, P. F., & Evans, A. D. (2006). Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. *Journal of Applied Ecology*, 43(2), 209–218. doi: 10.1111/j.1365-2664.2006.01146.x
- Duffy, J. E., Godwin, C. M., & Cardinale, B. J. (2017). Biodiversity effects in the wild are common and as strong as key drivers of productivity. *Nature*, 549(7671), 261–264. doi: 10.1038/nature23886
- Ehrmann, S., Liira, J., Gärtner, S., Hansen, K., Brunet, J., Cousins, S. A. O., ... Scherer-Lorenzen, M. (2017). Environmental drivers of *Ixodes ricinus* abundance in forest fragments of rural European landscapes. *BMC Ecology*, 17(1). doi: 10.1186/s12898-017-0141-0
- Estreguil, C., Caudullo, G., de Rigo, D., & San Miguel, J. (2013). Forest landscape in Europe: pattern, fragmentation and connectivity. *EUR Scientific and Technical Research*, 25717. Retrieved from http://vwb-xforest.jrc.it/media/cms_page_media/53/2012-fragmentation_executive%20rep_EUR25717.doc.pdf
- Ewers, R. M., & Banks-Leite, C. (2013). Fragmentation impairs the microclimate buffering effect of tropical forests. *PLOS ONE*, 8(3), e58093. doi: 10.1371/journal.pone.0058093
- Fahrig, L. (2013). Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography*, 40(9), 1649–1663. doi: 10.1111/jbi.12130
- Fahrig, L. (2017). Ecological responses to habitat fragmentation per se. *Annual Review of Ecology, Evolution, and Systematics*, 48(1), 1–23. doi: 10.1146/annurev-ecolsys-110316-022612
- Felipe-Lucia, M. R., Soliveres, S., Penone, C., Manning, P., Plas, F. van der, Boch, S., ... Allan, E. (2018). Multiple forest attributes underpin the supply of multiple ecosystem services. *Nature Communications*, 9(1), 4839. doi: 10.1038/s41467-018-07082-4
- Flinn, K. M., & Vellend, M. (2005). Recovery of forest plant communities in post-agricultural landscapes. *Frontiers in Ecology and the Environment*, 3(5), 243–250.

- Frey, S. J., Hadley, A. S., Johnson, S. L., Schulze, M., Jones, J. A., & Betts, M. G. (2016). Spatial models reveal the microclimatic buffering capacity of old-growth forests. *Science Advances*, *2*(4), e1501392.
- Gamfeldt, L., Hillebrand, H., & Jonsson, P. R. (2008). Multiple functions increase the abundance of biodiversity for overall ecosystem functioning. *Ecology*, *89*(5), 1223–1231. doi: 10.1890/06-2091.1
- Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., ... Bengtsson, J. (2013). Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications*, *4*, 1340. doi: 10.1038/ncomms2328
- Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., ... Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, *1*(2), e1500052–e1500052. doi: 10.1126/sciadv.1500052
- Hall, S. J. G., & Bunce, R. G. H. (2011). Mature trees as keystone structures in Holarctic ecosystems – a quantitative species comparison in a northern English park. *Plant Ecology & Diversity*, *4*(2–3), 243–250. doi: 10.1080/17550874.2011.586735
- Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., ... Loveland, T. R. (2013). High-resolution global maps of 21st-century forest cover change. *Science*, *342*(6160), 850–853.
- Herrera, J. M., & García, D. (2009). The role of remnant trees in seed dispersal through the matrix: being alone is not always so sad. *Biological Conservation*, *142*(1), 149–158.
- Hunter, M. L. (2017). Conserving small natural features with large ecological roles: An introduction and definition. *Biological Conservation*, *211*, 1–2. doi: 10.1016/j.biocon.2016.12.019
- Jamoneau, A., Chabrierie, O., Closset-Kopp, D., & Decocq, G. (2012). Fragmentation alters beta-diversity patterns of habitat specialists within forest metacommunities. *Ecography*, *35*(2), 124–133. doi: 10.1111/j.1600-0587.2011.06900.x
- Jonsell, M. (2012). Old park trees as habitat for saproxylic beetle species. *Biodiversity and Conservation*, *21*(3), 619–642. doi: 10.1007/s10531-011-0203-0
- Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*(5), 573–579. doi: 10.1111/2041-210X.12512
- Lefcheck, J. S., Byrnes, J. E. K., Isbell, F., Gamfeldt, L., Griffin, J. N., Eisenhauer, N., ... Duffy, J. E. (2015). Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. *Nature Communications*, *6*, 6936. doi: 10.1038/ncomms7936

- Lenoir, J., Hattab, T., & Pierre, G. (2017). Climatic microrefugia under anthropogenic climate change: implications for species redistribution. *Ecography*, *40*(2), 253–266. doi: 10.1111/ecog.02788
- Lindenmayer, D. B. (2017). Conserving large old trees as small natural features. *Biological Conservation*, *211*, 51–59. doi: 10.1016/j.biocon.2016.11.012
- MacArthur, R. H., & Wilson, E. O. (1967). The theory of island biogeography. *Princeton, New Jersey*.
- Manning, A. D., Gibbons, P., & Lindenmayer, D. B. (2009). Scattered trees: a complementary strategy for facilitating adaptive responses to climate change in modified landscapes? *Journal of Applied Ecology*, *46*(4), 915–919.
- Manning, Adrian D., Fischer, J., & Lindenmayer, D. B. (2006). Scattered trees are keystone structures – Implications for conservation. *Biological Conservation*, *132*(3), 311–321. doi: 10.1016/j.biocon.2006.04.023
- Mitchell, M. G. E., Bennett, E. M., & Gonzalez, A. (2014). Forest fragments modulate the provision of multiple ecosystem services. *Journal of Applied Ecology*, *51*(4), 909–918. doi: 10.1111/1365-2664.12241
- Mitchell, M. G. E., Suarez-Castro, A. F., Martinez-Harms, M., Maron, M., McAlpine, C., Gaston, K. J., ... Rhodes, J. R. (2015). Reframing landscape fragmentation's effects on ecosystem services. *Trends in Ecology & Evolution*. doi: 10.1016/j.tree.2015.01.011
- Naaf, T., & Kolk, J. (2015). Colonization credit of post-agricultural forest patches in NE Germany remains 130–230 years after reforestation. *Biological Conservation*, *182*, 155–163. doi: 10.1016/j.biocon.2014.12.002
- Pe'er, G., Dicks, L. V., Visconti, P., Arlettaz, R., Báldi, A., Benton, T. G., ... Scott, A. V. (2014). EU agricultural reform fails on biodiversity. *Science*, *344*(6188), 1090–1092. doi: 10.1126/science.1253425
- Penone, C., Allan, E., Soliveres, S., Felipe-Lucia, M. R., Gossner, M. M., Seibold, S., ... Fischer, M. (2019). Specialisation and diversity of multiple trophic groups are promoted by different forest features. *Ecology Letters*, *22*(1), 170–180. doi: 10.1111/ele.13182
- Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. (2016). *nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-128*.
- R Core Team. (2018). *R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>*.

- Remy, E., Wuyts, K., Van Nevel, L., De Smedt, P., Boeckx, P., & Verheyen, K. (2018). Driving factors behind litter decomposition and nutrient release at temperate forest edges. *Ecosystems*, *21*(4), 755–771. doi: 10.1007/s10021-017-0182-4
- Remy, E., Wuyts, K., Verheyen, K., Gundersen, P., & Boeckx, P. (2018). Altered microbial communities and nitrogen availability in temperate forest edges. *Soil Biology and Biochemistry*, *116*, 179–188. doi: 10.1016/j.soilbio.2017.10.016
- Scherber, C., Eisenhauer, N., Weisser, W. W., Schmid, B., Voigt, W., Fischer, M., ... Tschardt, T. (2010). Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature*, *468*(7323), 553–556. doi: 10.1038/nature09492
- Shipley, B. (2009). Confirmatory path analysis in a generalized multilevel context. *Ecology*, *90*(2), 363–368. doi: 10.1890/08-1034.1
- Suding, K. N., Lavorel, S., Chapin, F. S., Cornelissen, J. H. C., Díaz, S., Garnier, E., ... Navas, M.-L. (2008). Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology*, *14*(5), 1125–1140. doi: 10.1111/j.1365-2486.2008.01557.x
- Thompson, P. L., & Gonzalez, A. (2016). Ecosystem multifunctionality in metacommunities. *Ecology*, *97*(10), 2867–2879. doi: 10.1002/ecy.1502
- Valdés, A., Lenoir, J., Gallet-Moron, E., Andrieu, E., Brunet, J., Chabrierie, O., ... Decocq, G. (2015). The contribution of patch-scale conditions is greater than that of macroclimate in explaining local plant diversity in fragmented forests across Europe. *Global Ecology and Biogeography*, *24*(9), 1094–1105. doi: 10.1111/geb.12345
- van der Plas, F., Manning, P., Allan, E., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., ... Fischer, M. (2016). Jack-of-all-trades effects drive biodiversity–ecosystem multifunctionality relationships in European forests. *Nature Communications*, *7*, 11109. doi: 10.1038/ncomms11109
- Vanneste, T., Valdés, A., Verheyen, K., Perring, M. P., Bernhardt-Römermann, M., Andrieu, E., ... De Frenne, P. (2019). Functional trait variation of forest understorey plant communities across Europe. *Basic and Applied Ecology*, *34*, 1–14. doi: 10.1016/j.baae.2018.09.004

- Weathers, K. C., Cadenasso, M. L., & Pickett, S. T. A. (2001). Forest edges as nutrient and pollutant concentrators: potential synergisms between fragmentation, forest canopies and the atmosphere. *Conservation Biology*, *15*(6), 1506–1514. doi: 10.1046/j.1523-1739.2001.01090.x
- Winfree, R., W. Fox, J., Williams, N. M., Reilly, J. R., & Cariveau, D. P. (2015). Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters*, *18*(7), 626–635. doi: 10.1111/ele.12424
- Zoderer, B. M., Tasser, E., Carver, S., & Tappeiner, U. (2019). Stakeholder perspectives on ecosystem service supply and ecosystem service demand bundles. *Ecosystem Services*, *37*, 100938. doi: 10.1016/j.ecoser.2019.100938

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 hypothetical
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 5×5 km².

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.

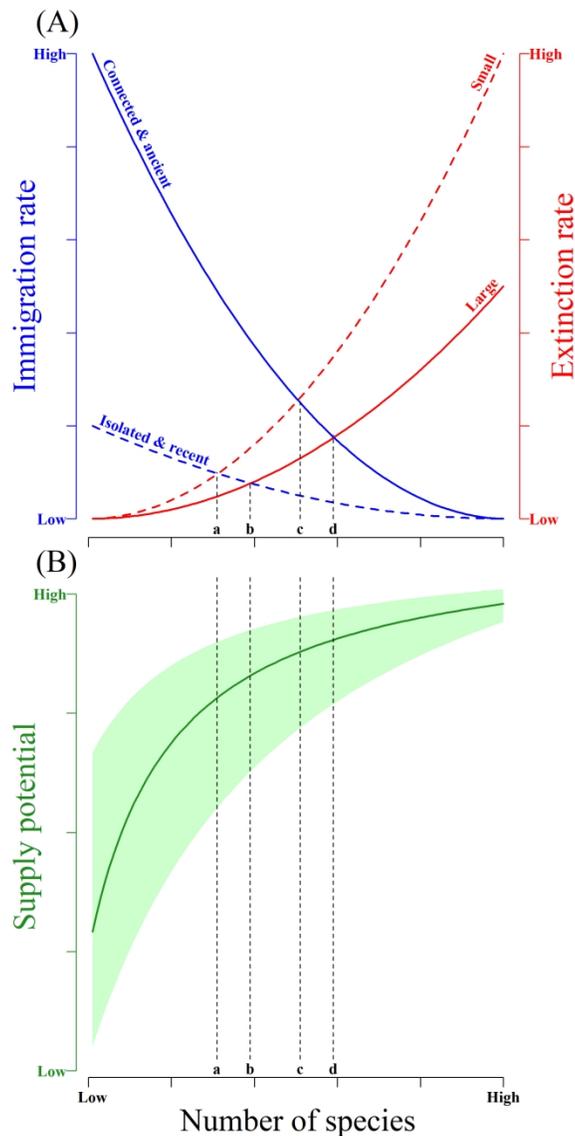


Figure 1: Linking island biogeography (MacArthur & Wilson, 1967) and ecosystem functioning for studying the supply potential of multiple ecosystem services by small forest patches. Hypothetical framework on the effects of forest continuity across space and over time on immigration and extinction rates, 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)

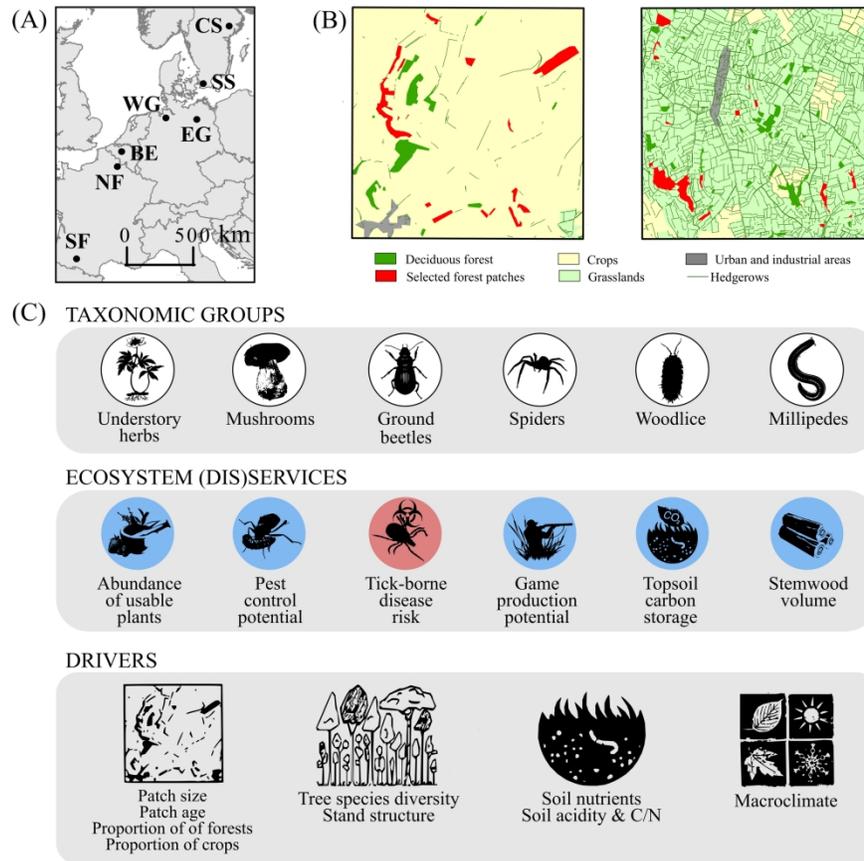


Figure 2: Sampling biodiversity and ecosystem services in small forest patches in agricultural landscapes. (A) Sampling locations along the 2500-km latitudinal gradient in Europe (SF = South France, NF = North France, BE = Belgium, WG = West Germany, EG = East Germany, SS = South Sweden, CS = Central 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 km². (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 × 300 DPI)

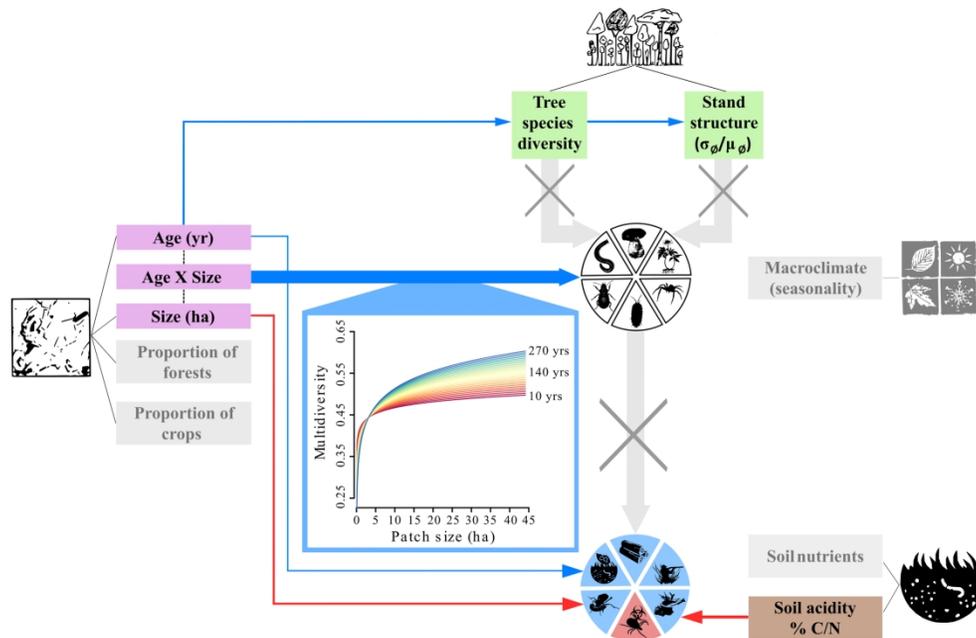


Figure 3: Linkage between the environment, biodiversity and high-performance multiservice delivery in small woodlands across Europe. Results of the piecewise structural equation model (piecewise SEM, $p = 0.512$) studying the response of high-performance multiservice (MS) delivery to multidiversity, 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)

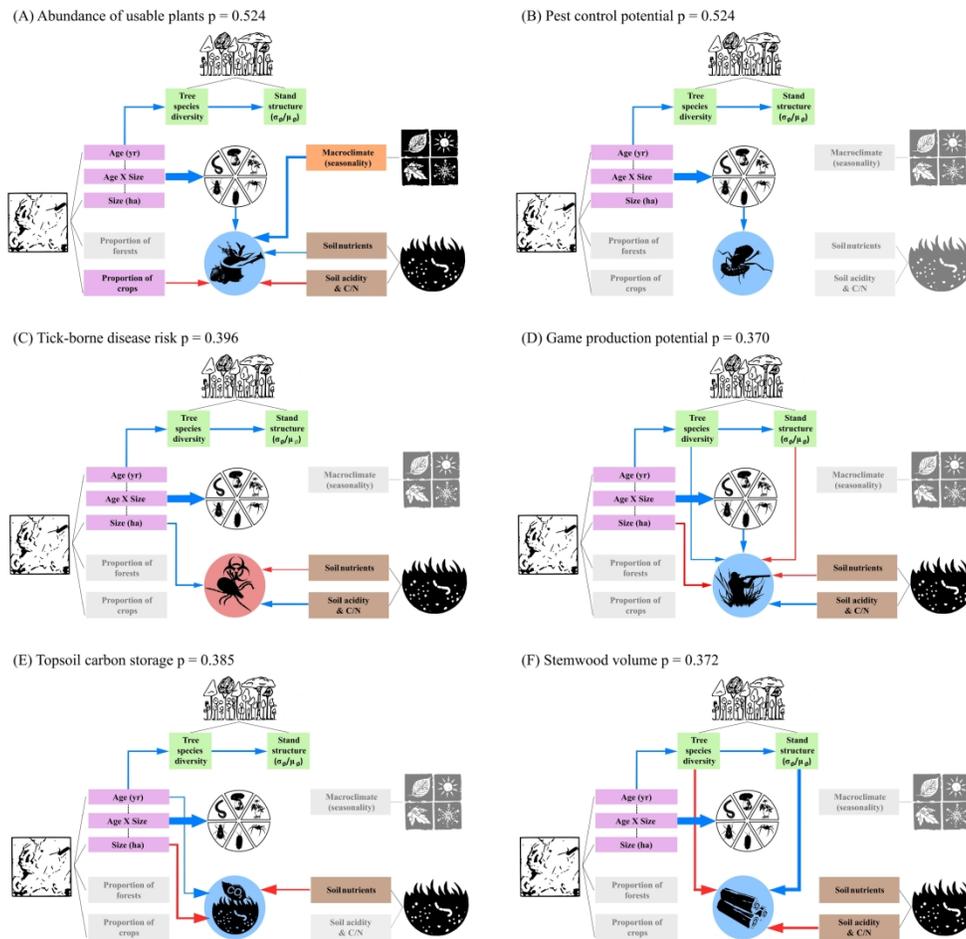


Figure 4: Linkage between the environment, biodiversity and individual ecosystem services in small woodlands across Europe. Results of the piecewise structural equation models studying the response of each individual ecosystem service to multidiversity, patch size, historical age and connectivity (proportion 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 m²) 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 cm² 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 (CaCl₂) 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 HClO₄ (65%), HNO₃ (70%) and H₂SO₄ (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⁻¹), the C:N ratio, the total P content (kg ha⁻¹)
46 and the pH (CaCl₂) 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 m²) was assessed using a standardized sampling protocol.
164 All ticks stages were collected via drag sampling (Tack et al., 2011) with a 1 × 1 m²
165 piece of white flannel fabric attached to a wooden pole on a 100-m long transect
166 (resulting in a 100 m² 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 (m³) 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*

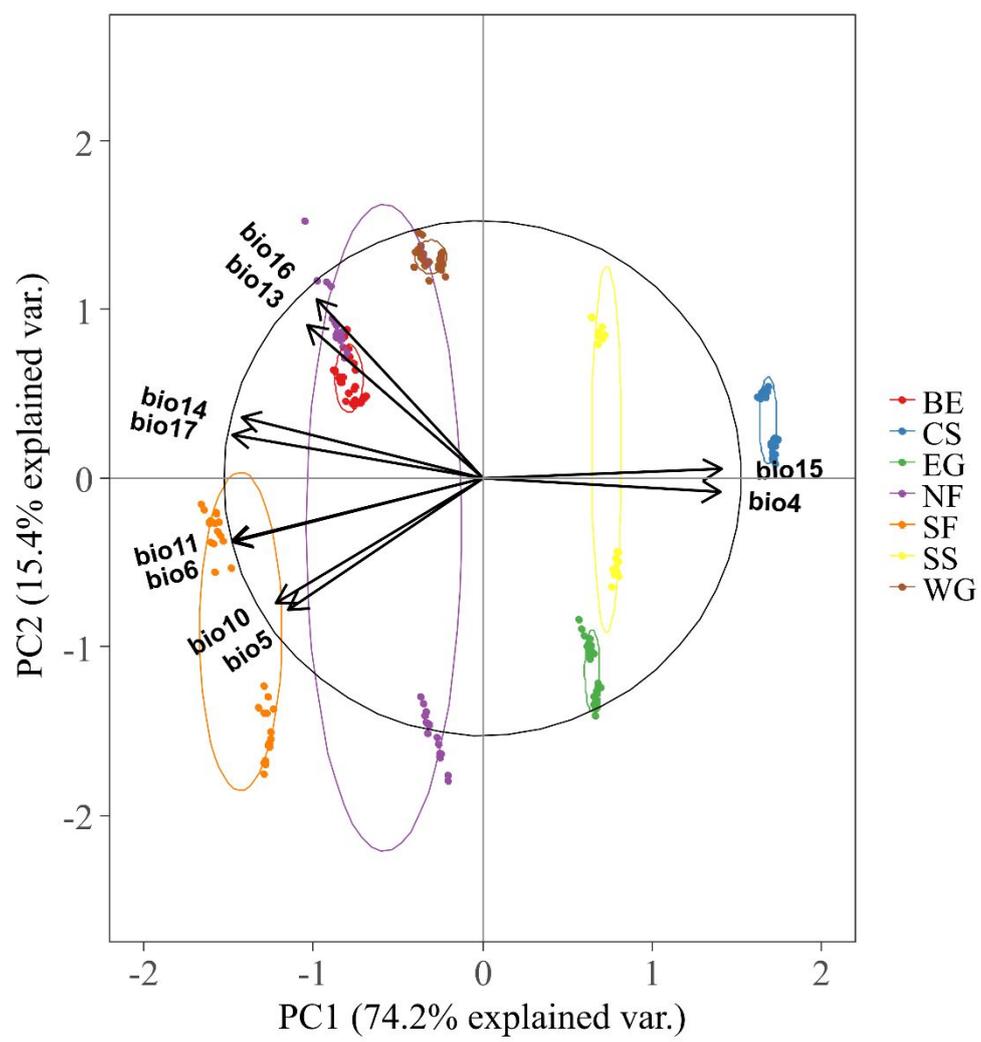
183 We used the soil C content (Mg/ha) in the combined forest floor and mineral topsoil (10
184 cm) for each patch as a measure of the potential for topsoil carbon storage.

185 REFERENCES

- 186 Bon, M. (2012). Champignons de France et d'Europe. Flammarion.
- 187 Bonet, J. A., Pukkala, T., Fischer, C. R., Palahí, M., De Aragón, J. M., & Colinas, C.
188 (2008). Empirical models for predicting the production of wild mushrooms in Scots
189 pine (*Pinus sylvestris* L.) forests in the Central Pyrenees. *Annals of Forest Science*,
190 65(2), 206–206.
- 191 Cottam, G., & Curtis, J. T. (1956). The use of distance measures in phytosociological
192 sampling. *Ecology*, 37(3), 451. Doi:10.2307/1930167
- 193 Courtecuisse, R., & Duhem, B. (2013). Champignons de France et d'Europe. Paris :
194 Delachaux et Niestlé.
- 195 Deleuze, C., Morneau, F., Renaud, J. P., Vivien, Y., Rivoire, M., Santenoise, P., ...
196 Vallet, P. (2014). Estimer le volume total d'un arbre, quelles que soient l'essence, la
197 taille, la sylviculture, la station. *Rendez-Vous Techniques ONF*, (44), 22–32.

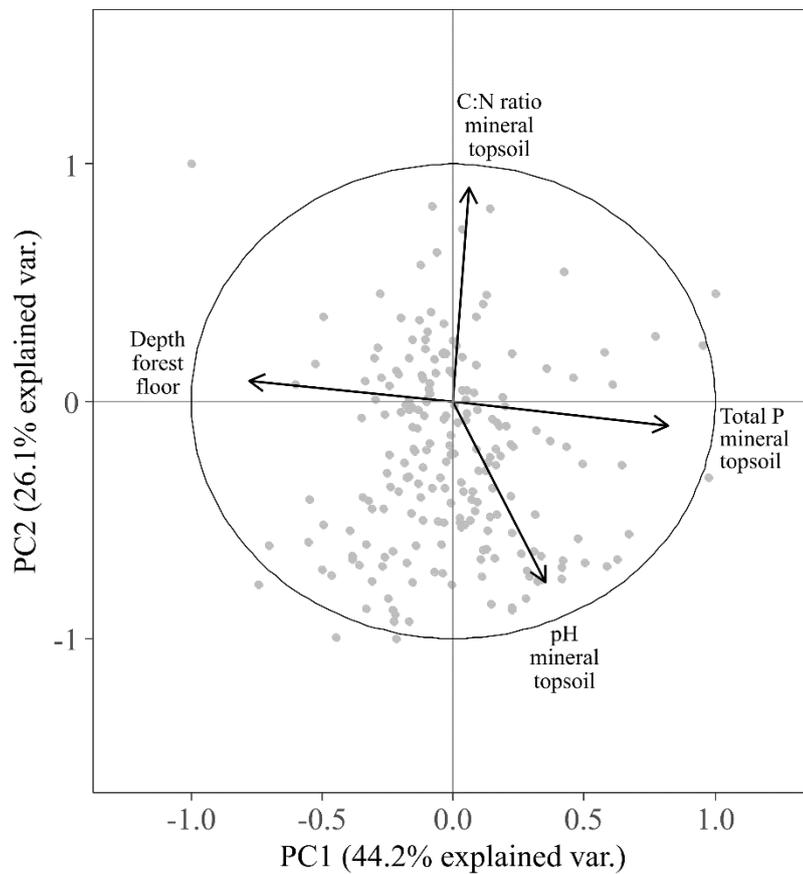
- 198 Ehrmann, S., Liira, J., Gärtner, S., Hansen, K., Brunet, J., Cousins, S. A. O., ... Scherer-
199 Lorenzen, M. (2017). Environmental drivers of *Ixodes ricinus* abundance in forest
200 fragments of rural European landscapes. *BMC Ecology*, 17, 31. Doi:10.1186/s12898-
201 017-0141-0
- 202 Eyssartier, G., & Roux, P. (2013). *Le Guide des champignons – France et Europe (3^e*
203 *édition)*. Paris: Belin literature et revues.
- 204 Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., ...
205 Bengtsson, J. (2013). Higher levels of multiple ecosystem services are found in
206 forests with more tree species. *Nature Communications*, 4, 1340.
207 Doi:10.1038/ncomms2328
- 208 Lajtha, K., Driscoll, C. T., Jarrell, W. M., & Elliott, E. T. (1999). Soil phosphorus:
209 characterization and total element analysis. In *Standard soil methods for long-term*
210 *ecological research*. New York: Oxford University Press. P (pp. 115–42).
- 211 Lovari, S., Serrao, G., & Mori, E. (2017). Woodland features determining home range
212 size of roe deer. *Behavioural Processes*, 140, 115–120.
- 213 Tack, W., Madder, M., Frenne, P. D., Vanhellefont, M., Gruwez, R., & Verheyen, K.
214 (2011). The effects of sampling method and vegetation type on the estimated
215 abundance of *Ixodes ricinus* ticks in forests. *Experimental and Applied Acarology*,
216 54(3), 285–292. Doi:10.1007/s10493-011-9444-6
- 217 Tansley, A. G. (1935). The use and abuse of vegetational concepts and terms. *Ecology*,
218 16(3), 284–307.

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.



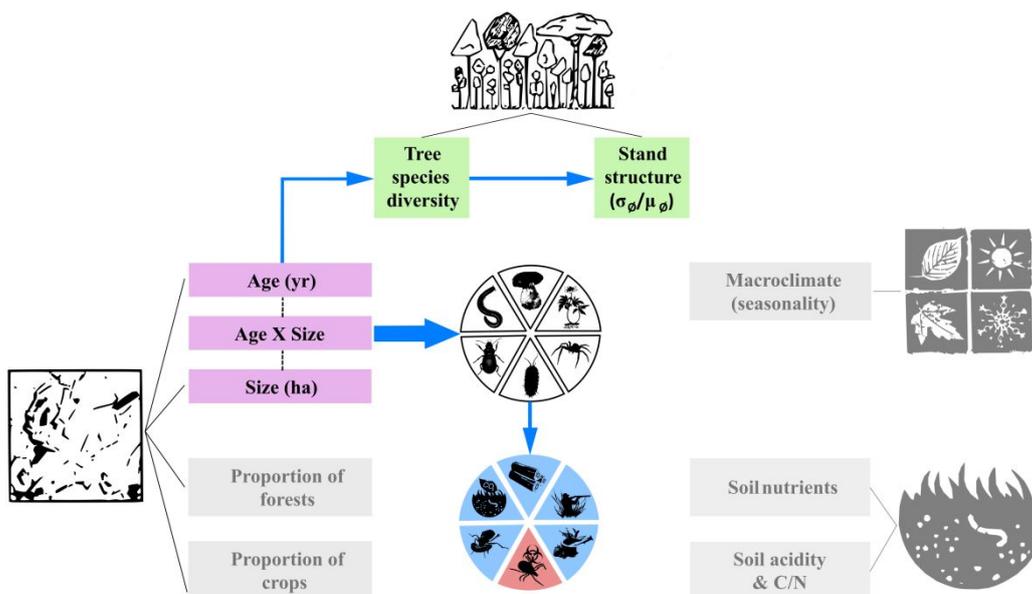
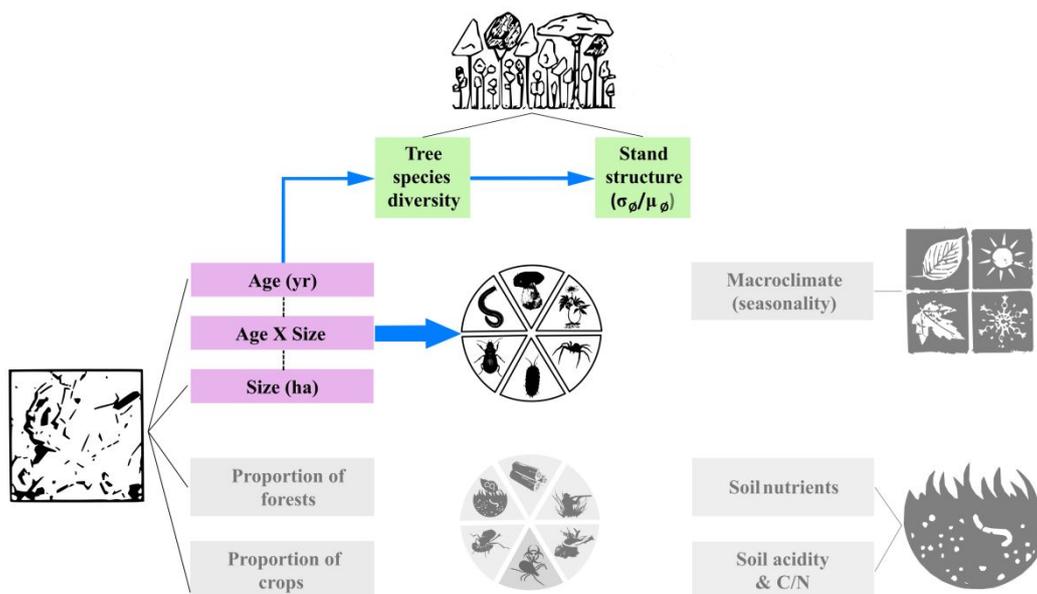
232

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

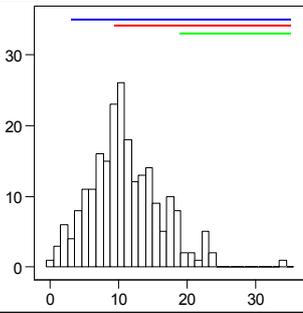
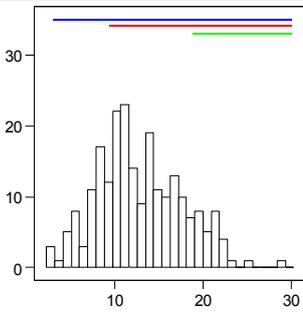
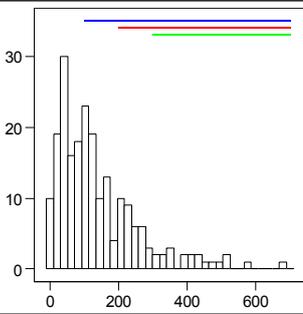
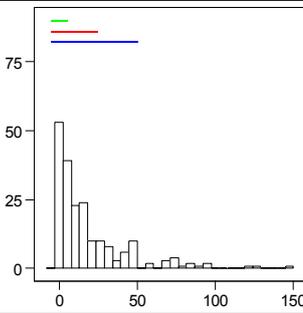
	small	recent	4	0.41	0.17	17.16	10.32
Fr_S_O	large	old	5	9.04	2.99	125.44	6.4
	large	recent	3	4.27	1.66	12	0
	small	old	4	1.18	0.48	88.86	50.69
	small	recent	4	0.55	0.18	12	0
Ge_E_B	large	old	8	5.8	3.42	122.27	69
	large	recent	0	-	-	-	-
	small	old	1	2.48	-	70.51	-
	small	recent	7	1.14	0.39	12	0
Ge_E_O	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

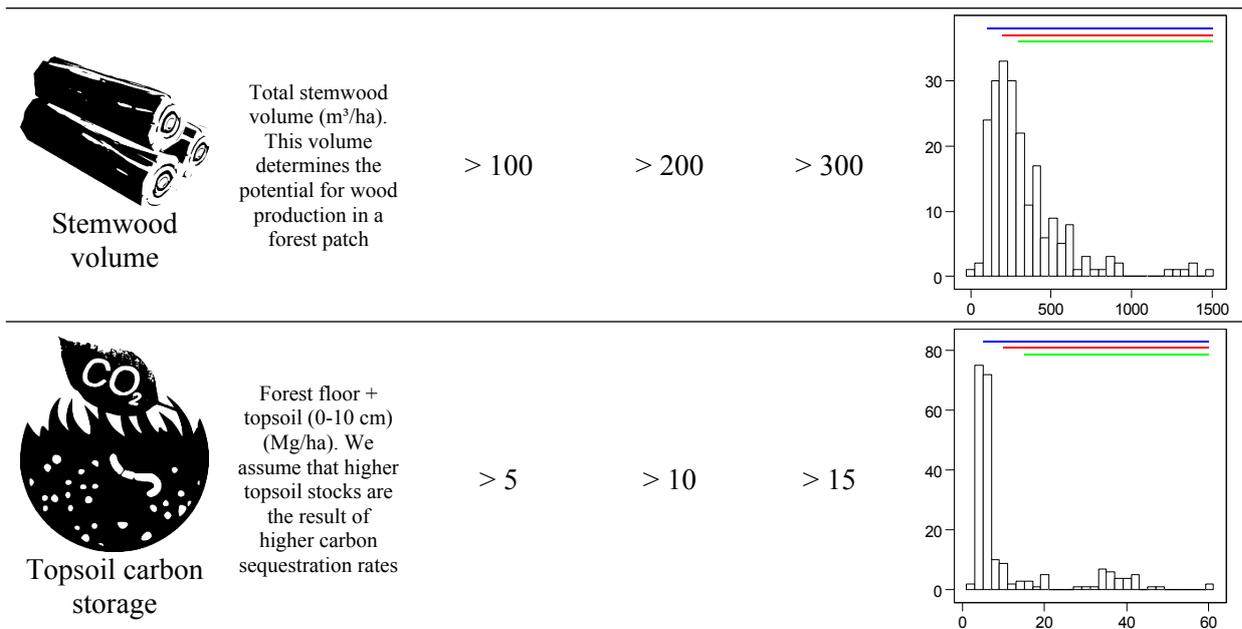
Sw_C_O	large	old	4	2.74	1.84	125.85	95.19
	large	recent	4	4.78	5.79	12	0
	small	old	4	0.62	0.2	48.09	14.82
	small	recent	4	0.64	0.19	17.08	10.17
Sw_S_B	large	old	10	9.48	10.32	202.9	53
	large	recent	2	2.14	0	57.98	65.02
	small	old	1	0.38	-	107.6	-
	small	recent	3	0.86	0.33	35.04	18.31
Sw_S_O	large	old	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 m²) 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 m². 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 ²). 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 ² (i.e. value of 3.14)	> 1 dominant species per 100 m ² (i.e. 9.42)	> 2 dominant species per 100 m ² (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 ² (i.e. value of 3.14)	> 1 dominant species per 100 m ² (i.e. 9.42)	> 2 dominant species per 100 m ² (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 ² . Density of nymphs determines the density of Borrelia-infected nymphs, which is a key proxy for disease risk	< 50	< 25	< 5	



277

278 REFERENCES

- 279 Food and Agriculture Organization of the United States (FAO) (2015a). Global Forest
 280 Resources Assessment 2015: How are the world's forests changing? Retrieved from
 281 <http://www.fao.org/forest-resources-assessment/en/>
- 282 Food and Agriculture Organization of the United States (FAO) (2015b). Global Forest
 283 Resources Assessment 2015. Desk reference. Retrieved from
 284 <http://www.fao.org/forest-resources-assessment/en/>
- 285 Rouabah, A., Villerd, J., Amiaud, B., Plantureux, S., & Lasserre-Joulin, F. (2015).
 286 Response of carabid beetles diversity and size distribution to the vegetation structure
 287 within differently managed field margins. *Agriculture, Ecosystems & Environment*,
 288 *200*, 21–32. doi: 10.1016/j.agee.2014.10.011
- 289 Ruyts, S. C., Tack, W., Ampoorter, E., Coipan, E. C., Matthysen, E., Heylen, D., ...
 290 Verheyen, K. (2018). Year-to-year variation in the density of *Ixodes ricinus* ticks and

291 the prevalence of the rodent-associated human pathogens *Borrelia afzelii* and *B.*
292 *miyamotoi* in different forest types. *Ticks and Tick-Borne Diseases*, 9(2), 141–145.

293 Tansley, A. G. (1935). The use and abuse of vegetational concepts and terms. *Ecology*,
294 16(3), 284–307.

295 Vesterdal, L., Schmidt, I. K., Callesen, I., Nilsson, L. O., & Gundersen, P. (2008).
296 Carbon and nitrogen in forest floor and mineral soil under six common European tree
297 species. *Forest Ecology and Management*, 255(1), 35–48. doi:
298 10.1016/j.foreco.2007.08.015

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		

313

314 REFERENCES

315 Couplan, F. (2009). *Le régal végétal: plantes sauvages comestibles* (Vol. 1). Editions

316 Ellebore.

317 Ducerf, G. (2013). *L'encyclopédie des plantes bio-indicatrices alimentaires et*318 *médicinales: guide de diagnostic des sols*. Promonature.319 Mabey, R., & Blamey, M. (1989). *Food for free*. Collins.320 Mears, R., & Hillman, G. C. (2007). *Wild food*. Hodder & Stoughton.321 Toby, G., Denham, A., & Whitelegg, M. (2016). *The Western herbal tradition: 2000*322 *years of medicinal plant knowledge*. Singing Dragon.

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:
 325 Barančeková, 2004; Barančeková, Krojerová-Prokešová, Šustr, & Heurich, 2010;
 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, & Hjermmann, 1999; Schmidt, Sommer,
 330 Kriebitzsch, Ellenberg, & Oheimb, 2004; Storms et al., 2008; Tixier et al., 1997; and
 331 Wallach, Shanas, & Inbar, 2010.

Species name

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

332

333 REFERENCES

334 Barančková, M. (2004). The roe deer diet: is floodplain forest optimal habitat? *Folia*
335 *Zool*, 53(3), 285–292.

336 Barančková, M., Krojerová-Prokešová, J., Šustr, P., & Heurich, M. (2010). Annual
337 changes in roe deer (*Capreolus capreolus* L.) diet in the Bohemian Forest, Czech
338 Republic/Germany. *European Journal of Wildlife Research*, 56(3), 327–333.
339 doi:10.1007/s10344-009-0321-0

340 Bartolomé, J., Rosell, C., & Bassols, E. (2002). Diet composition of roe deer
341 (*Capreolus capreolus*) in the Natural Park of the Garrotxa volcanic zone (Catalonia,
342 Spain). *Pirineos*, 157(0), 57–64. doi:10.3989/pirineos.2002.v157.61

343 Cederlund, G., & Nyström, A. (1981). Seasonal differences between moose and roe
344 deer in ability to digest browse. *Holarctic Ecology*, 4(1), 59–65.

345 Czernik, M., Taberlet, P., Świsłocka, M., Czajkowska, M., Duda, N., & Ratkiewicz, M.
346 (2013). Fast and efficient DNA-based method for winter diet analysis from stools of
347 three cervids: moose, red deer, and roe deer. *Acta Theriol*, 58, 379–386.

348 de Jong, C. B., Gill, R. M. A., van Wieren, S. E., & Burlton, F. W. E. (1995). Diet
349 selection by roe deer *Capreolus capreolus* in Kielder Forest in relation to plant
350 cover. *Forest Ecology and Management*, 79(1–2), 91–97. doi:10.1016/0378-
351 1127(95)03622-9

- 352 Helle, P. (1980). Food composition and feeding habits of the roe deer in winter in
353 central Finland. *Acta Theriologica*, 25(32), 395–402.
- 354 Henry, B. A. M. (1975). *Dispersion, diet and criteria of age of roe deer (Capreolus*
355 *capreolus L.) in Hamsterley forest, county Durham* (Doctoral). Durham University.
356 Retrieved from <http://etheses.dur.ac.uk/8178/>
- 357 Jackson, J. (1980). The annual diet of the roe deer (*Capreolus capreolus*) in the New
358 Forest, Hampshire, as determined by rumen content analysis. *Journal of Zoology*,
359 192(1), 71–83. doi:10.1111/j.1469-7998.1980.tb04220.x
- 360 Kamler, J., & Homolka, M. (2005). Faecal nitrogen: a potential indicator of red and roe
361 deer diet quality in forest habitats. *Folia Zoologica Praha*, 54(1/2), 89.
- 362 Maizeret, C., Boutin, J.-M., Cibien, C., & Carlino, J.-P. (1989). Effects of population
363 density on the diet of roe deer and the availability of their food in Chizé forest. *Acta*
364 *Theriol*, 34, 235–246.
- 365 Moser, B., Schütz, M., & Hindenlang, K. E. (2008). Resource selection by roe deer: Are
366 windthrow gaps attractive feeding places? *Forest Ecology and Management*, 255(3–
367 4), 1179–1185. doi:10.1016/j.foreco.2007.10.023
- 368 Mysterud, A., Lian, L.-B., & Hjermann, D. Ø. (1999). Scale-dependent trade-offs in
369 foraging by European roe deer (*Capreolus capreolus*) during winter. *Canadian*
370 *Journal of Zoology*, 77, 1486–1493.
- 371 Schmidt, M., Sommer, K., Kriebitzsch, W.-U., Ellenberg, H., & Oheimb, G. von.
372 (2004). Dispersal of vascular plants by game in northern Germany. Part I: Roe deer
373 (*Capreolus capreolus*) and wild boar (*Sus scrofa*). *European Journal of Forest*
374 *Research*, 123(2), 167–176. doi:10.1007/s10342-004-0029-3

- 375 Storms, D., Aubry, P., Hamann, J.-L., Saïd, S., Fritz, H., Saint-Andrieux, C., & Klein,
376 F. (2008). Seasonal variation in diet composition and similarity of sympatric red deer
377 *Cervus elaphus* and roe deer *Capreolus capreolus*. *Wildlife Biology*, 14(2), 237–250.
378 doi:10.2981/0909-6396(2008)14[237:SVIDCA]2.0.CO;2
- 379 Tixier, H., Duncan, P., Scehovic, J., Yant, A., Gleizes, M., & Lila, M. (1997). Food
380 selection by European roe deer (*Capreolus capreolus*): effects of plant chemistry,
381 and consequences for the nutritional value of their diets. *Journal of Zoology*, 242(2),
382 229–245. doi:10.1111/j.1469-7998.1997.tb05799.x
- 383 Wallach, A. D., Shanas, U., & Inbar, M. (2010). Feeding activity and dietary
384 composition of roe deer at the southern edge of their range. *European Journal of*
385 *Wildlife Research*, 56(1), 1–9. doi:10.1007/s10344-009-0281-4

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.

Species name

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 nigrita
Pterostichus oblongopunctatus
Semiophonus signaticornis
Trechus gr. Quadristriatus
Trechus secalis

386

387 REFERENCES

- 388 Bohan, D. A., Bohan, A. C., Glen, D. M., Symondson, W. O., Wiltshire, C. W., &
389 Hughes, L. (2000). Spatial dynamics of predation by carabid beetles on slugs.
390 *Journal of Animal Ecology*, 69(3), 367–379.
- 391 Brandmayr, P., & Brandmayr, T. Z. (1986). Food and feeding behaviour of some
392 *Licinus* species (Coleoptera Carabidae Licinini). *Monitore Zoologico Italiano-Italian*
393 *Journal of Zoology*, 20(2), 171–181.

- 394 Cornic, J. F. (1973). Etude du regime alimentaire de trois especes de Carabiques et de
395 ses variations en verger de pomiers. *Ann. Soc. Ent. France*, 9, 69–87.
- 396 Dajoz, R. (2002). *The Coleoptera. Carabids and tenebrionids: ecology and biology*.
397 Éditions Tec & Doc.
- 398 Davies, M. J. (1953). The contents of the crops of some British carabid beetles.
399 *Entomologist's Monthly Magazine*, 89, 18–23.
- 400 Dennison, D. F., & Hodkinson, I. D. (1983). Structure of the predatory beetle
401 community in a woodland soil ecosystem. I. Prey selection. *Pedobiologia*, 25(2),
402 109–115.
- 403 Fawki, S., & Toft, S. (2005). Food preferences and the value of animal food for the
404 carabid beetle *Amara similata* (Gyll.)(Col., Carabidae). *Journal of Applied*
405 *Entomology*, 129(9-10), 551–556.
- 406 Grimm, B., Paill, W., & Kaiser, H. (2000). The " Spanish slug": autecology, predators
407 and wild plants as food plants. *Förderungsdienst*, 48(1), 11–16.
- 408 Gruntal, S. Y., & Sergeyeva, T. K. (1989). Food relations characteristics of the beetles
409 of the genera *Carabus* and *Cychrus*. *Zoologicheskij Zhurnal. Moscow*, 58(1), 45–51.
- 410 Henderson, I. F., Andino, D., Peairs, E., Mazier, F., López, C., Cantoral Flores, O., ...
411 Bhat, P. K. (1996). *Slug and snail pests in agriculture. Monograph No. 66*. British
412 Crop Protection Council, Surrey (RU).
- 413 Holland, J. M. (2002). *The agroecology of carabid beetles*. Intercept Limited.
- 414 Jelaska, L. S., Franjevic, D., JelASKA, S. D., & Symondso, W. O. (2014). Prey
415 detection in carabid beetles (Coleoptera: Carabidae) in woodland ecosystems by PCR
416 analysis of gut contents. *European Journal of Entomology*, 111(5), 631.

- 417 Kromp, B. (1999). Carabid beetles in sustainable agriculture: a review on pest control
418 efficacy, cultivation impacts and enhancement. *Agriculture, Ecosystems &*
419 *Environment*, 74(1), 187–228.
- 420 Loreau, M. (1984). Etude expérimentale de l'alimentation de *Abax ater* Villers,
421 *Carabus problematicus* Herbst et *Cychus attenuatus* Fabricus (Coleoptera:
422 Carabidae). *Annales de La Societe Royale Zoologique de Belgique*, 114, 227–240.
- 423 Loreau, Michel. (1983). Le régime alimentaire de huit carabides (Coleoptera) communs
424 en milieu forestier. *Acta Oecologica. Oecologia Generalis*, 4(4), 331–343.
- 425 McKemey, A. R., Symondson, W. O. C., Glen, D. M., & Brain, P. (2001). Effects of
426 slug size on predation by *Pterostichus melanarius* (Coleoptera: Carabidae).
427 *Biocontrol Science and Technology*, 11(1), 81–91.
- 428 Mitchell, B. (1963). Ecology of two carabid beetles, *Bembidion lampros* (Herbst) and
429 *Trechus quadristriatus* (Schrank). *The Journal of Animal Ecology*, 377–392.
- 430 Pakarinen, E. (1994). The importance of mucus as a defence against carabid beetles by
431 the slugs *Arion fasciatus* and *Deroceras reticulatum*. *Journal of Molluscan Studies*,
432 60(2), 149–155.
- 433 Poulin, G., & O'Neil, L. G. (1969). Observations sur les prédateurs de la limace noire,
434 *Arion ater* (L.) (Gastéropodes, Pulmonés, Arionidés). *Phytoprotection*, 50, 1–6.
- 435 Ribera, I., Foster, G. N., Downie, I. S., McCracken, D. I., & Abernethy, V. J. (1999). A
436 comparative study of the morphology and life traits of Scottish ground beetles
437 (Coleoptera, Carabidae). *Annales Zoologici Fennici*, 21–37.
- 438 Scherney, F. (1960). Beiträge zur Biologie und ökonomischen Bedeutung räuberisch
439 lebender Käferarten. *Journal of Applied Entomology*, 47(1-4), 231–255.

- 440 Scherney, F. (2003). *Unsere Laufkäfer: ihre Biologie und wirtschaftliche Bedeutung*.
441 Westarp Wissenschaftenverlagsgesellschaft.
- 442 Sergeyeva, T. K., & Gryuntal, S. Y. (1990). Relationships of ground beetles,
443 *Pterostichus*, species with their food resources. *Entomological Review (USA)*.
- 444 Symondson, W. O. (2004). Coleoptera (Carabidae, Staphylinidae, Lampyridae, Drilidae
445 and Silphidae) as predators of terrestrial gastropods. *Natural Enemies of Terrestrial*
446 *Molluscs*. Oxford, UK, CAB International, 37–84.
- 447 Symondson, W. O. C. (1989). Biological control of slugs by carabids. In *Henderson, I.*
448 *F. (ed.) Slugs and Snails in World Agriculture, BCPC Monograph 41. British Crop*
449 *Protection Council, Surrey, UK. (pp. 295–300)*.
- 450 Symondson, W. O. C., Glen, D. M., Wiltshire, C. W., Langdon, C. J., & Liddell, J. E.
451 (1996). Effects of cultivation techniques and methods of straw disposal on predation
452 by *Pterostichus melanarius* (Coleoptera: Carabidae) upon slugs (Gastropoda:
453 Pulmonata) in an arable field. *Journal of Applied Ecology*, 741–753.
- 454 Symondson, W. O. C., & Liddell, J. E. (1993). The detection of predation by *Abax*
455 *parallelepipedus* and *Pterostichus madidus* (Coleoptera: Carabidae) on Mollusca
456 using a quantitative ELISA. *Bulletin of Entomological Research*, 83(4), 641–647.
- 457 Symondson, W. O. C., & Liddell, J. E. (1996). A species-specific monoclonal antibody
458 system for detecting the remains of field slugs, *Deroceras reticulatum*
459 (Muller)(Mollusca: Pulmonata), in carabid beetles (Coleoptera: Carabidae).
460 *Biocontrol Science and Technology*, 6(1), 91–100.
- 461 Tod, M. E. (1973). Notes on beetle predators of molluscs. *Entomologist*, 106(1324),
462 196–201.

463 Zhavoronkova, T. N. (1969). Certain structural peculiarities of the Carabidae
464 (Coleoptera) in relation to their feeding habits. *Entomological Review*, 48, 462–471.



1422x691mm (72 x 72 DPI)