1 TITLE: "High ecosystem service delivery potential of small woodlands in agricultural

2 landscapes"

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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*. Large, ancient woodlands host high levels of biodiversity

57   and can therefore deliver a number of ecosystem services. In contrast, 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, small woodlands

61   are not currently considered by public policies. There is thus an urgent need for

62   targeted policy instruments to ensure 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.

INTRODUCTION

Forests deliver a wide range of ecosystem services to human society, and positive

relationships between biodiversity and these services have been reported for large forested

areas (Gamfeldt et al., 2013; van der Plas et al., 2016). However, there is a lack of knowledge

about the relationship between biodiversity and multiple ecosystem services in small

woodland patches (Decocq et al., 2016; Mitchell, Bennett, & Gonzalez, 2014). Indeed, in

many parts of the world, the original forest cover has been heavily fragmented (Haddad et al.,

2015; Hansen et al., 2013) due to human activities; more than 70% of the remaining global

forest cover lies within 1 km of a forest edge (Haddad et al., 2015). Many of the remaining

woodlands are smaller than 10 ha (Estreguil, Caudullo, de Rigo, & San Miguel, 2013) and

scattered in a human-transformed matrix of mostly arable lands, pastures and human

settlements. Loss of area, increased isolation and greater exposure to human disturbances

along forest edges are leading causes of biodiversity loss (Haddad et al., 2015), although

small patch size can sometimes be beneficial for biodiversity, as shown by the preponderance

of positive significant responses to habitat fragmentation (Fahrig, 2017).

Small woodland patches in agricultural landscapes also vary in age, since many of

them have developed on farmland that was abandoned at different points in time (Flinn &

Vellend, 2005). Consequently, small woodlands not only differ in size and degree of isolation,

but also in age, quantified as the time since forest establishment, ranging from very ancient

(several centuries or older) to more recent (less than a century). Despite their small size and

isolation, patches of (semi-)natural habitats such as small and ancient woodlands can have an

important role as refugia for biodiversity (Decocq et al., 2016) and as providers of multiple

ecosystem services (Decocq et al., 2016; Mitchell et al., 2014). Therefore, small and ancient

forest patches, analogously to other "small natural features" (Hunter, 2017) such as scattered

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., 2015),

109 the functional diversity of patches is expected to vary as well since traits of species colonizing

110 and persisting in, for instance, small, young or isolated patches will differ from those

111 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 WorldClim

179   global database (1-km resolution, http://www.worldclim.org/) and averaged each variable for

180   each patch using all pixels intersecting with the patch area. We performed a principal

181   components analysis (PCA, Fig. S1) on these 10 variables representing seasonality and

182   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:

$$MD = average\left[\left(\frac{UH_i}{\overline{UH}_{5\,highest}} + \frac{MU_i}{\overline{MU}_{5\,highest}} + \frac{CB_i}{\overline{CB}_{5\,highest}} + \frac{SP_i}{\overline{SP}_{5\,highest}} + \frac{MI_i}{\overline{MI}_{5\,highest}} + \frac{WO_i}{\overline{WO}_{5\,highest}}\right)\right]$$

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 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-transformed),

270   historical age (and their interaction term to account for the species-time-area

271   relationship; Adler et al. 2005), habitat availability (proportion of forests) and

272   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 in

324   more acidic soils with higher C:N ratio, while the abundance of usable plants and stemwood

325   volume decreased. Forest structure affected two proxies: game production potential increased

326   with tree species diversity and decreased with structural diversity, and stemwood volume,

327   which decreased with tree species diversity and increased with structural diversity. All

328   piecewise SEM models reported here were consistent with the data ($p > 0.05$ in all cases).

329   DISCUSSION

330   We showed that multidiversity was highest in large and ancient forest patches. Multiservice

331   delivery potential at high performance levels per area was maximal in the smallest and most

332   ancient woodlands and was not affected by multidiversity, which only influenced multiservice

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

334   services.

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

336   *delivery potential*

337   Our results show that, although larger and more ancient woodlands hosted a higher

338   biodiversity, as predicted by the species-time-area relationship (Adler et al., 2005), this was

339   unrelated to a high-performance multiservice delivery potential. Contrary to our expectations,

340   high-performance multiservice delivery potential decreased as patch size increased,

341   independent of the positive effect of patch size on multidiversity. This means that smaller

342   woodlands potentially deliver multiple services at higher performance levels on a per area

343   basis than larger woodlands of a similar age, even if the larger woodlands harbor a higher

344   biodiversity. This unexpected result may be explained by the positive edge effect on the

345   delivery potential of some ecosystem services (Bodin et al., 2006; Mitchell et al., 2014). As

346   smaller woodlands have a relatively high edge-to-core ratio (Ewers & Banks-Leite, 2013;

347   Weathers, Cadenasso, & Pickett, 2001), they are highly exposed to external influences; they

348   receive, for example, proportionally more light penetrating through the edge, a warmer and

349   drier microclimate and more nutrient input from surrounding agricultural lands compared to

350   large forests. These conditions promote, among others, higher patch-level microclimate

351   heterogeneity (Frey et al., 2016) as well as a more dense vegetation cover and an increased

352   biomass production at forest edges (Remy, Wuyts, Van Nevel, et al., 2018; Remy, Wuyts,

353   Verheyen, Gundersen, & Boeckx, 2018) in small woodlands. This altered functioning in turn

354   increases the delivery potential of some services, such as game production potential, due to an

355   increased quantity of food available for game, and topsoil carbon storage, due to the faster

356   incorporation of organic matter in the soil. Tick-borne disease risk is, however, lower, likely

357   due to decreased larval densities in the unfavorable (e.g. hotter and drier) microclimatic

358   conditions at the edge (Ehrmann et al., 2017).

359   On the other hand, the positive and indirect interaction effect of patch size and age,

360   mediated by a higher multidiversity, increased multiservice delivery potential at a low-

361   performance level, as well as some individual ecosystem services. Therefore, it seems that the

362   higher biodiversity hosted by larger and more ancient woodlands is able to maintain a

363   minimal level of multiservice supply potential, while the maintenance of higher levels is less

364   dependent on the amount of biodiversity. The supply potential of several individual ecosystem

365   services indirectly increased in larger and more ancient woodlands because it was dependent

366   on higher levels of biodiversity. For example, abundance of usable plants and game

367   production potential might have increased due to a positive correlation with vascular plant

368   diversity, while pest control potential probably increased due to bottom-up effects through the

369   trophic chain (Scherber et al., 2010). On the contrary, tick-borne disease risk, topsoil carbon

370   storage and stemwood volume were unrelated to multidiversity, probably because they

371   depended on particular environmental conditions or on the presence and abundance of

372   specific species (Winfree, Fox, Williams, Reilly, & Cariveau, 2015) rather than on species

373   richness *per se*.

374   Finally, it should be noted that we focused on the service delivery potential on a per

375   area basis and that the total amount of services provided by large patches might still be larger

376   than that of small patches. Our findings should therefore not be interpreted as a trade-off

377   between large, biodiverse patches versus small patches that have a higher potential to deliver

378   services, but rather as an observation that small woodlands in agricultural landscapes have the

379   potential to deliver a high flow of services relative to their size.

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

381 The amount of forest cover around each woodland (cf. the habitat amount hypothesis, Fahrig,

382 2013) had no effect on multidiversity, multiservice delivery potential and individual services,

383 which indicates that habitat availability within the landscape did not influence the service

384 supply potential. This lack of effect may be a consequence of the disruption of

385 metacommunity functioning in highly fragmented systems, with the dispersal of species

386 among small forest patches dramatically reduced (Jamoneau, Chabrerie, Closset-Kopp, &

387 Decocq, 2012). Both models (Thompson & Gonzalez, 2016) and experiments (Haddad et al.,

388 2015) predict reduced multifunctionality in such highly fragmented systems. The delivery of

389 some ecosystem services may decline with low habitat connectivity, and with an intensively

390 managed landscape matrix, as we have observed for the abundance of usable plants, which

391 decreased with the proportion of crops surrounding the forest patch. Such an effect most

392 likely results from a greater exposure of the forest edges to the biocides and fertilizers used in

393 the adjacent croplands (Chabrerie, Jamoneau, Gallet-Moron, & Decocq, 2013).

394 Macroclimatic conditions affected neither multidiversity nor multiservice delivery

395 potential, although we studied a large climatic gradient covering the entire European

396 temperate biome. Only one of the individual services, the abundance of usable plants, was

397 positively affected by macroclimate seasonality, increasing towards northern latitudes. This

398 overall lack of effects of macroclimate suggests that the expected major biogeographic

399 gradients influencing ecosystem service delivery potential are lost in highly fragmented forest

400 ecosystems, at least partly due to the loss of macroclimate-driven biodiversity gradients

401 (Valdés et al., 2015, Vanneste et al., 2019) and a decoupling between sub-canopy and free-air

402 temperatures (De Frenne et al., 2013, 2019; Frey et al., 2016; Lenoir, Hattab, & Pierre, 2017).

403 Similarly, other potentially influential microclimate factors such as soil moisture and relative

404 air humidity, not assessed in this study, could contribute to the observed lack of effects of

405 macroclimate on multidiversity and multiservice delivery.

406   *Future research avenues*

407   This study is a first step towards a better understanding of the factors that influence the

408   biodiversity and multiservice delivery potential of woodland patches in agricultural

409   landscapes. Obviously, not all possible services were considered here (see Decocq et al. 2016

410   for an overview) and this raises the question of whether inclusion of other services, like

411   erosion control and water quality regulation, both acting at a landscape scale, would alter the

412   results. This is not unlikely, since it has been shown that different services are underpinned by

413   different forest attributes (Felipe-Lucia et al., 2018). Next, inclusion of more driving

414   variables, e.g. those that quantify the past and current management and the microclimate in

415   the patches, may help to further clarify how human actions in these patches influence their

416   biodiversity and ecosystem service delivery potential. Another research avenue along the

417   same lines is making the step from ecosystem service delivery potential towards actual

418   ecosystem delivery. Indeed, not all services play an equally important role in all landscapes or

419   for all stakeholders, and potential ecosystem service assessments should ideally be

420   complemented by socio-economic analyses quantifying the importance and value of the

421   studied services (e.g. Bagstad et al., 2014; Zoderer et al., 2019). Finally, such integrated

422   analyses will require the use of more sophisticated indicators that better reflect the actual

423   ecosystem services that are delivered than the indicators we used.

424   CONCLUSIONS

425   Our study responds to the call for empirical research into the nature of the relationships

426   between fragmentation and ecosystem service supply potential (Mitchell et al., 2015). We

427   have shown that both large and small woodland patches in agricultural landscapes fulfill

428   important roles. The large, ancient woodlands host the highest biodiversity and are

429   particularly important for conservation. They also have the potential to deliver a considerable

430   flow of services, but smaller woodlands have a higher potential to deliver multiple ecosystem

431 services on a per area basis than the larger woodlands, especially when they are ancient. This

432 higher potential of small woodlands might be caused by edge effects that can enhance the

433 delivery potential of several services. Preserving the small woodlands is hence important to

434 increase the multifunctionality of agricultural landscapes. This is an important finding

435 because especially the small woodlands are currently not included in major national and

436 international policies affecting biodiversity and ecosystem services in agricultural landscapes,

437 such as the EU Natura 2000 network, the EU water Directive and the Common Agricultural

438 Policy (Pe'er et al., 2014). Our findings advocate for the development of relevant policy

439 instruments in order to ensure their future conservation. Next, we also found that the

440 importance of drivers vary depending on performance levels of the ecosystem service and on

441 the individual (dis-)service considered. A given driver may thus affect individual services in

442 opposite directions, which leads to trade-offs among services (Gamfeldt et al., 2013; Lefcheck

443 et al., 2015; Felipe-Lucia et al., 2018). Consequently, different management strategies of these

444 woodlands would be required to achieve multiservice delivery at high performance levels or

445 to maximize (respectively minimize) the delivery of a specific ecosystem service (respectively

446 disservice). For some services and performance levels, biodiversity conservation and

447 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

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467 DATA AVAILABILITY STATEMENT

468 Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.cfxpnvx2c

469 (Valdés et al., 2019).

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470   Figure 1: Linking island biogeography (MacArthur & Wilson, 1967) and ecosystem

471   functioning for studying the supply potential of multiple ecosystem services by small forest

472   patches. Hypothetical framework on the effects of forest continuity across space and over

473   time on immigration and extinction rates, and thus on the level of biodiversity (i.e. total

474   number of species per forest patch) and the associated supply potential of multiple ecosystem

475   services. (A) MacArthur & Wilson's theory of island biogeography adapted to forest

476   spatiotemporal characteristics (effect of patch connectivity and age on immigration rate and of

477   patch size on extinction rate). (B) Theoretically expected relationship between species

478   richness and supply potential of multiple ecosystem services. The letters along the x-axis (a,

479   b, c and d) depict different landscapes with different expectations on species richness and thus

480   on supply potential of multiple ecosystem services, consisting of: (a) small, isolated and

481   recent forest patches (a lower species richness is expected); (b) large but isolated and recent

482   forest patches (intermediate levels of species richness are expected); (c) small but connected

483   and ancient forest patches (intermediate levels of species richness are expected); and (d) large,

484   connected and ancient forest patches (a higher species richness is expected). The green line

485   and the green shaded polygon depict the average expected relationship between species

486   richness and supply potential of multiple ecosystem services as well as the hypothetic

487   confidence interval of all possible shapes we can expect for this relationship, respectively.

488   Figure 2: Sampling biodiversity and ecosystem service supply potential in small forest

489   patches in agricultural landscapes. (A) Sampling locations along the 2500-km latitudinal

490   gradient in Europe (SF = South France, NF = North France, BE = Belgium, WG = West

491   Germany, EG = East Germany, SS = South Sweden, CS = Central Sweden). (B) Detail of two

492   of the 14 studied landscapes (low vs. high connectivity) in North France, showing the

493   distribution of land uses and the selected forest patches in red. Each landscape is 5×5 km^2.
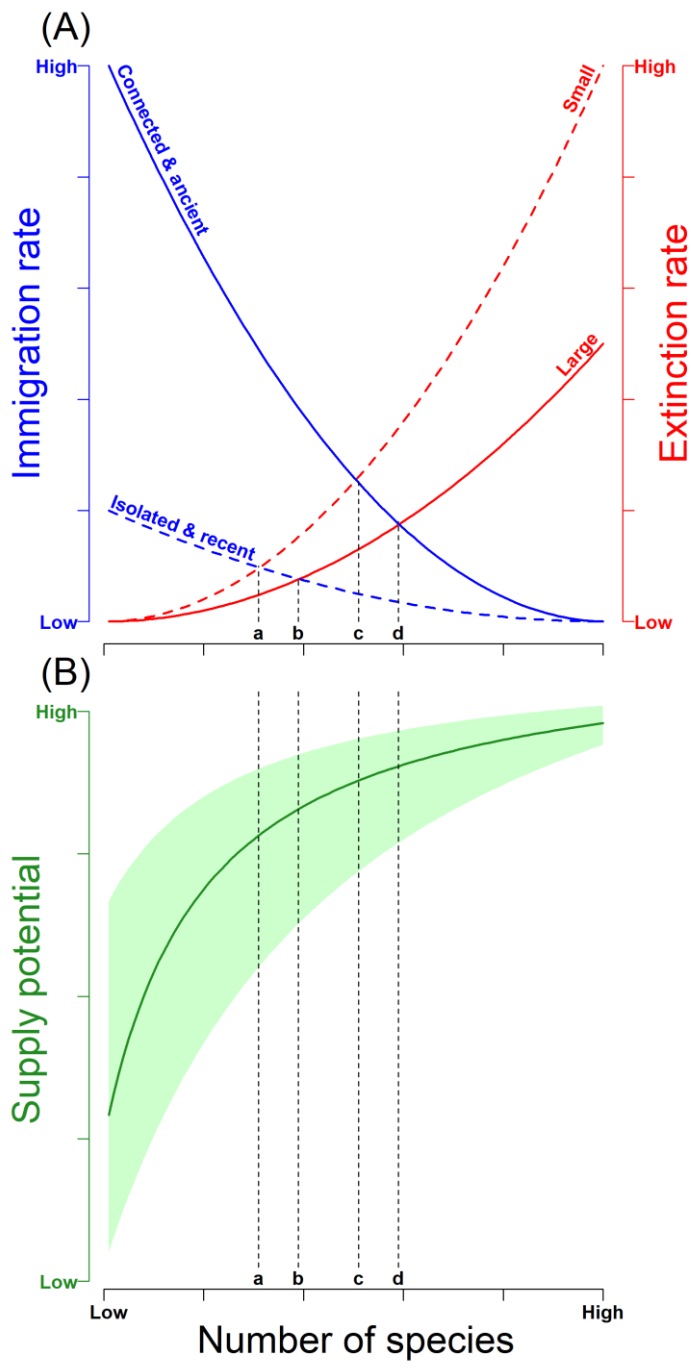
494   (C) Detail of the six taxonomic groups, six ecosystem services (blue) or disservices (red) and

495   four groups of drivers assessed within each of the selected forest patches.

496   Figure 3: Linkage between the environment, biodiversity and high-performance multiservice

497   delivery potential in small woodlands across Europe. Results of the piecewise structural

498   equation model (p = 0.512) studying the response of high-performance multiservice delivery

499   potential to multidiversity, patch size, age and connectivity (proportion of forests and crops in

500   a 500-m surface around each patch), while accounting for macroclimate, soil and forest

501   structural characteristics as environmental drivers. Blue arrows indicate positive effects and

502   red arrows indicate negative effects. Arrow thickness is proportional to the effect size. Only

503   significant paths (p < 0.05) are shown, while variables not significantly contributing to the

504   models are attenuated and represented with grey shading. Grey crossed arrows have been

505   included to highlight the lack of effects of multidiversity on multiservice, and of tree species

506   diversity and stand structure on multidiversity. The blue square depicts the positive interaction

507   effect (p = 0.03) between patch size and historical age on multidiversity, as predicted by the

508   species-time-area relationship. Marginal (i.e. fixed effects) and conditional (fixed plus random

509   effects) R^2 values are 0.33 and 0.48, respectively. The color ramp from red to blue depicts

510   different historical patch ages ranging from the youngest (10 yrs) to the oldest (270 yrs)

511   sampled patch ($n = 200$). All covariates (connectivity, macroclimate, soil and stand

512   conditions) in the model except patch size and historical age were set to their mean values.

513   Figure 4: Linkage between the environment, biodiversity and individual ecosystem service

514   supply potential in small woodlands across Europe. Results of the piecewise structural

515   equation models studying the response of each individual ecosystem service to multidiversity,

516   patch size, historical age and connectivity (proportion of forests and crops in a 500-m surface

517   around each patch), while accounting also for macroclimate, soil and forest structural

518   characteristics as environmental drivers. Blue arrows indicate positive effects and red arrows
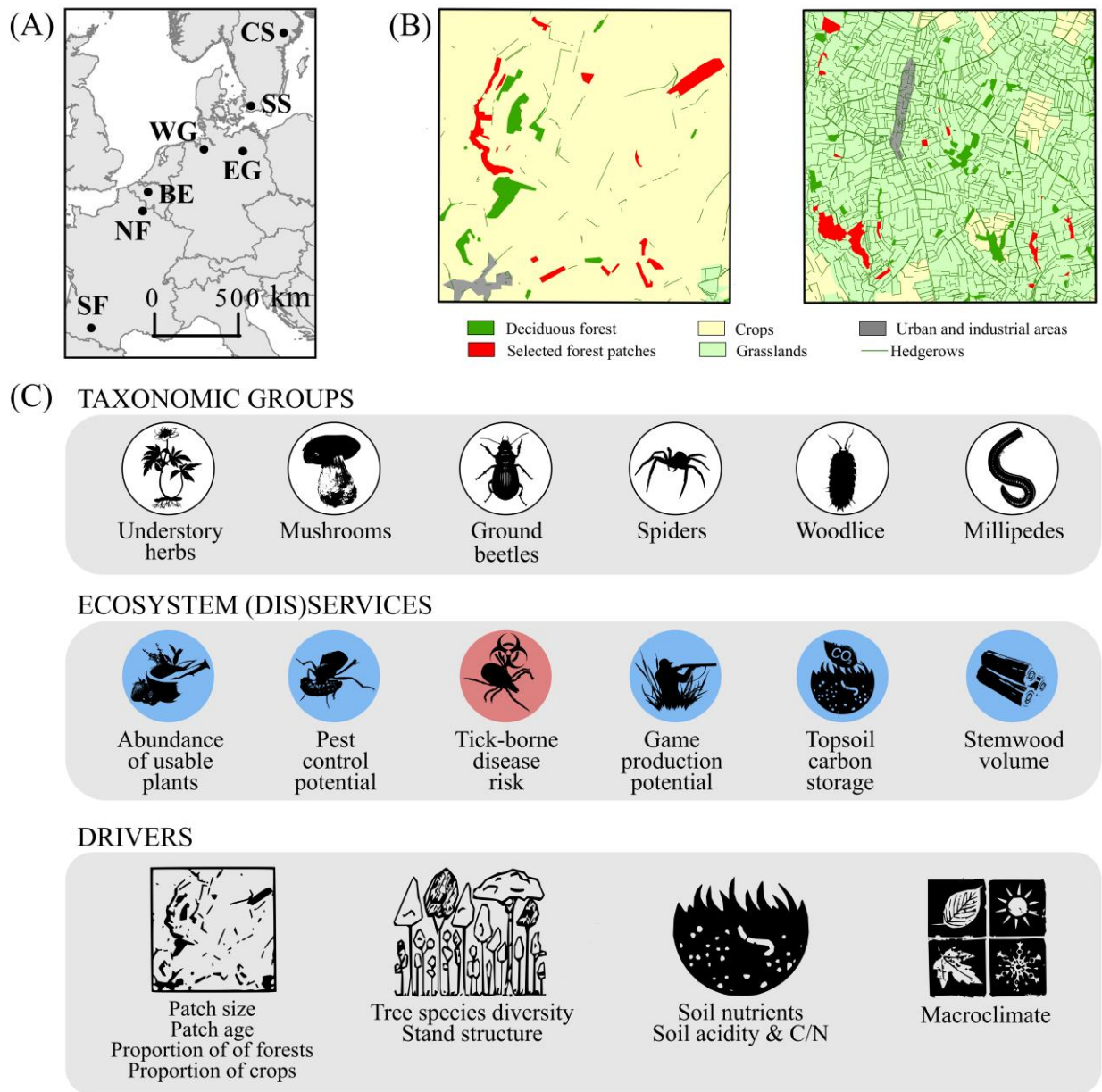
519 indicate negative effects. Arrow thickness is proportional to the effect size. Only significant

520 paths (p < 0.05) are shown, while variables not significantly contributing to the models are

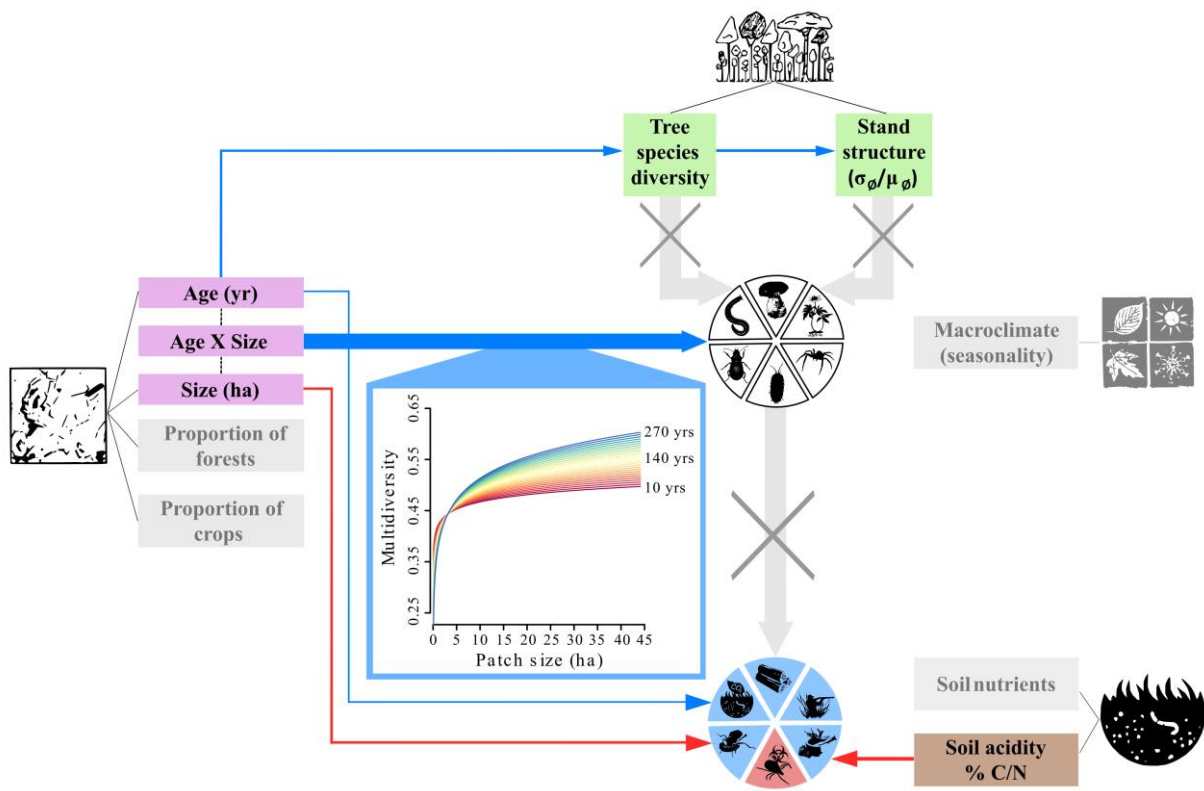521 attenuated and represented with grey shading. The overall p-value for each piecewise

522

(A)

High — Connected & ancient
Immigration rate
Isolated & recent
Low —

High — Small
Extinction rate
Large
Low —

a b c d

(B)

High —
Supply potential
Low —

a b c d

Low   Number of species   High

523

524   **Figure 1**

(A)

CS
SS
WG
EG
BE
NF
SF
0   500 km

(B)

Deciduous forest   Crops   Urban and industrial areas
Selected forest patches   Grasslands   Hedgerows

(C) TAXONOMIC GROUPS

Understory herbs   Mushrooms   Ground beetles   Spiders   Woodlice   Millipedes

ECOSYSTEM (DIS)SERVICES

Abundance of usable plants   Pest control potential   Tick-borne disease risk   Game production potential   Topsoil carbon storage   Stemwood volume

DRIVERS

Patch size
Patch age
Proportion of of forests
Proportion of crops

Tree species diversity
Stand structure

Soil nutrients
Soil acidity & C/N

Macroclimate

525

526   **Figure 2**

527

528 **Figure 3**

(A) Abundance of usable plants p = 0.524
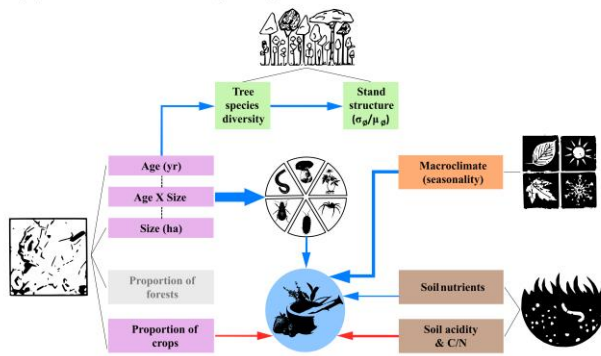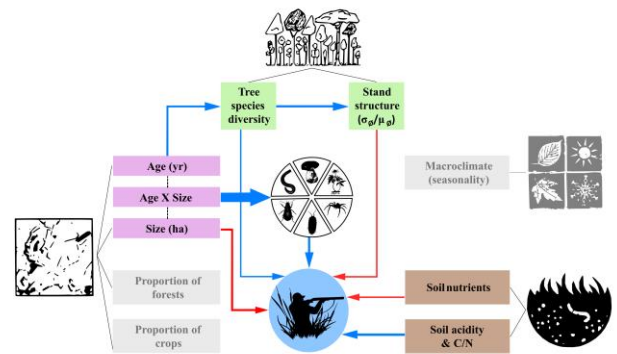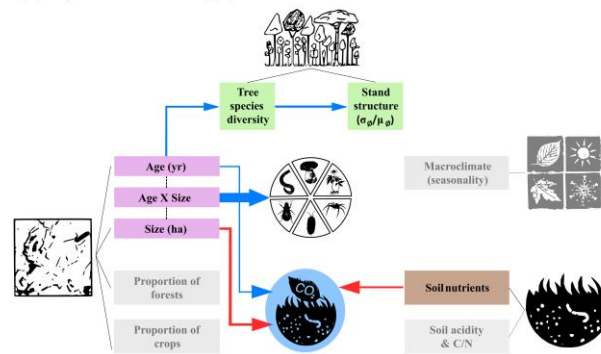
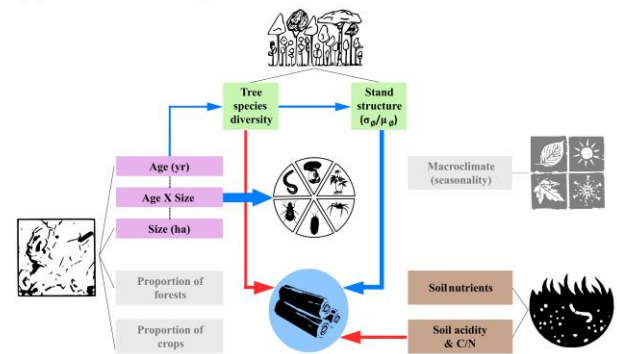(B) Pest control potential p = 0.524
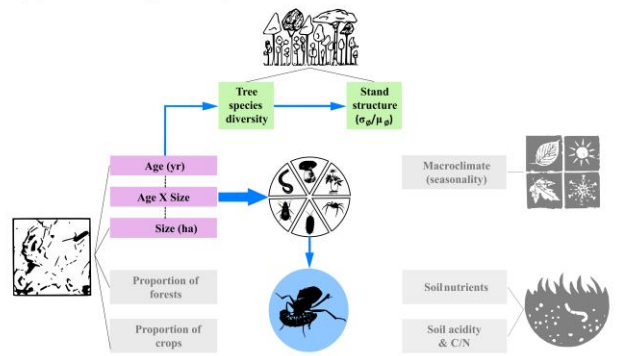
(C) Tick-borne disease risk p = 0.396
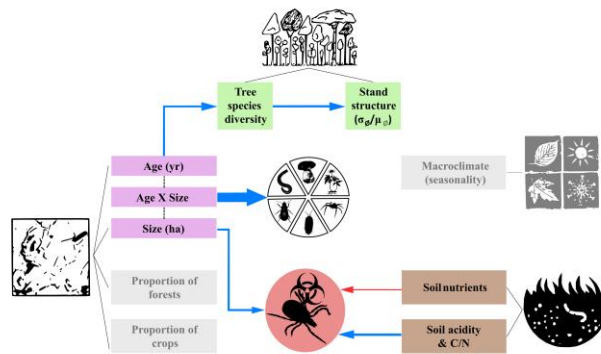
(D) Game production potential p = 0.370

(E) Topsoil carbon storage p = 0.385

(F) Stemwood volume p = 0.372

Figure 4

structural equation model (piecewise SEM) is shown in the heading of each panel.