Assessing the potential of routine stand variables from multi-taxon data as habitat surrogates in European temperate forests

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HAL Id: hal-02609972
https://hal.inrae.fr/hal-02609972

Submitted on 22 Oct 2021

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2   **European temperate forests**

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17

18   Abstract

19   To encourage forest managers to use biodiversity indicators in their work, providing environmental
20   variables that depict species habitats, have well-calibrated and strong relationships with biodiversity
21   and are easy to routinely record would be a step forward. The Index of Biodiversity Potential (IBP) is
22   a rapid habitat assessment method widely used in France. It uses ten variables that indicate potential
23   habitat for forest-dwelling species and is easy for forest managers to implement during their day-to-
24   day activities. The objective of this paper is to evaluate the indicator power of these IBP variables at
25   the stand scale, i.e. their capacity to co-vary with empirical species richness and composition data for
26   nine taxa. The data were obtained from 487 plots set up in 19 forested areas in France. Taxonomic
27   data focused on corticolous lichens, corticolous and saproxylic bryophytes, polypores, saproxylic
28   beetles, ground beetles, hoverflies, birds, bats and vascular plants. For the latter five taxa, we built
29   subgroups of forest-specialist species. The IBP variables were recorded on 1-ha circular plots
30   centered on the sampling point used to record taxonomic data. We explored the relationships
31   between the IBP variables and species composition/richness of nine taxa at the stand scale.
32   Furthermore, we searched for threshold values for all the significant relationships found between
33   species richness and the IBP variables. Variations in the species composition of vascular plants and
34   saproxylic beetles, and to a lesser extent, polypores, bats and lichens, were significantly related to
35   habitat variations (ranked according to the Procrustes significance level). The contribution of the IBP
36   variables to the total inertia of species composition was about 18.7% on average. The IBP variables

37 had a lower number of significant relationships with species richness than with species composition.
38 Unexpectedly, the forest subgroups mainly showed fewer significant relationships with habitat
39 variables than did the full-groups, both for species richness and composition. We highlighted seven
40 significant thresholds in the habitat variables above which species richness was significantly higher.
41 Finally, we recommend that forest managers (i) routinely use a rapid habitat assessment such as the
42 IBP, (ii) orient silvicultural practices to ensure conservation of autochtonous tree species, large logs
43 and different types of aquatic habitats above the thresholds highlighted in this study, and (iii)
44 periodically complete a biodiversity assessment at the forest scale by recording taxonomic data.

45

46 Key words: IBP; covariation; biodiversity; stand structure; species richness; species composition

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48 Highlights

49 • Composition of plants and saproxylic beetles assemblages co-varied with habitat variables
50 • The contribution of habitat variables to species composition inertia was relatively weak
51 • Forest subgroups showed weaker relationships with habitat variables than did full-taxa
52 • We found seven habitat thresholds above which species richness was significantly higher

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1. Introduction

Forests are crucial habitats for biodiversity since they support about two-thirds of the world's terrestrial biodiversity (WCFSD, 1999). In Europe, most forests have been managed for a long time (Larsson et al. 2001), and this has had a major impact on their biodiversity (e.g. Mitchell and Kirby 1989). The concept of sustainable forest management, which emerged at the 1992 Rio conference on Environmental Development, requires forest managers to maintain species diversity in managed areas (FAO 2015). However, taxonomic inventories are time-consuming and involve specialists, and therefore cannot be easily implemented by forest managers in their daily routine. Having said this, some quick, easy methods ("rapid habitat assessments") exist to survey key structural elements and succinctly describe the habitats typical of various forest taxa (Venier and Mackey 1997). Lindenmayer et al. (2000) suggested using environmental variables as biodiversity indicators. Testing and validating easy-to-record stand variables that depict species habitats and are relevant as biodiversity indicators would encourage forest managers to integrate these indicators into their typical working activities. . Larsson et al. (2001) proposed a list of key compositional, structural and functional environmental factors for each main European forest type. In the same way, Lindenmayer et al. (2006) suggested using keystone elements to improve and monitor eco-friendly forest management. Their focus was mainly on deadwood and tree-related microhabitats (TreMs) (Tews et al. 2004; Kraus and Krumm 2013). Composite indices, based on large-scale field data available from state forest inventories, have already been used in habitat assessment protocols (e.g. The Stand-scale Forest Biodiversity Index, Van Den Meersschaut and Vandekerkhove, 1998; the Austrian Forest Biodiversity Index, Geburek et al. 2010; The Biotope Value of the Forest Stand, WSL 2001). At the local (i.e. stand) scale, other indicator lists exist (e.g. Indicators of High Conservation Value Forest, Jennings et al. 2003; the European forest scorecards, Sollander 2000; The Rapid Appraisal of Riparian Condition, Jansen et al. 2004).

Unfortunately, the studies to date have not identified habitat indicators that are fully relevant for all taxa and all forest contexts (e.g. Bouget et al. 2014a; Van Den Meersschaut and Vandekerkhove 1998), and significant relationships between structural indicators and taxa has clearly been shown in only a very limited number of cases (Gao et al. 2015). Furthermore, most previous studies have focused on species richness, while the relationships between indicators and species composition have been poorly studied (Gao et al. 2015). Finally, Gao et al. (2015) recommended that environmental variables be further validated for forest ecosystems.

86   We chose to focus on species subgroups such as forest specialists (Gosselin 2012), since they are

87   often the main targets of forest conservation, and to emphasize the stand scale, since it is the main

88   operational scale for forest managers (Failing and Gregory 2003). The habitat variables the most

89   commonly tested at the stand scale in previous studies have been tree age, tree canopy cover,

90   deadwood volume and deadwood diversity (Gao et al. 2015). Few studies have tested other variables

91   such as shrub cover, vertical stratification, stand basal area, tree height, volume of standing trees,

92   TreMs or tree species composition (Gao et al. 2014; Gao et al. 2015). However, most of these

93   variables require not only field measurements but also subsequent calculations. The objective of our

94   study was to evaluate habitat variables that are easy to record in the field without specialized devices

95   and that do not require post-calculations for their indicator power at the stand scale. We therefore

96   used the ten variables already selected for a rapid habitat assessment method designed for routine

97   use in the field: the Index of Biodiversity Potential (IBP; Larrieu and Gonin 2008). The IBP index is

98   already being used in France by many forest managers. It combines ten factors deemed to favor

99   biodiversity, most of which focus on precise items either already typically observed by managers for

100   economic issues, or easy to observe in the field without any tools or devices. We investigated the

101   relationships between empirical species richness and composition data for nine taxa according to

102   these ten variables.

103

104   **2. Material and methods**

105   Taxonomic data were recorded following standardized procedures at the stand level, within the

106   framework of several different research projects (Table A1 in Supplementary Material). We used data

107   from 487 plots situated in 19 French forested areas (Fig 1). The wide range of forest contexts

108   sampled represented both the Atlantic and Continental zones, forests from lowlands to highlands,

109   and broadleaved, conifer-dominated and mixed stands (Fig. 1 and Table A2 in Supp. Mat.)

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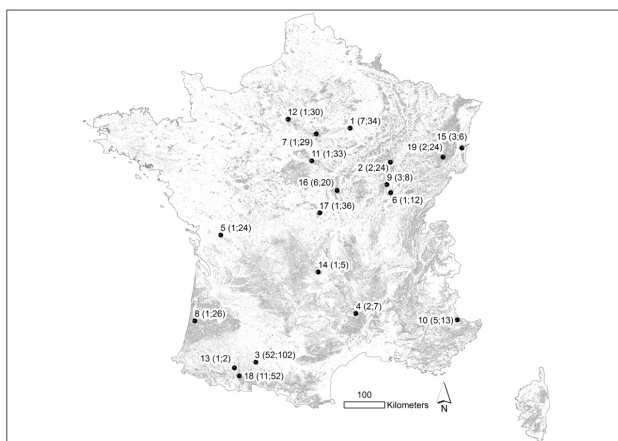
111

112   Fig. 1. Map of the 19 forested areas sampled; in brackets for each area, the number of forests

113   sampled followed by the number of sampling plots; 1:Aube, 2:Auberive, 3:Coteaux de Gascogne,

114   4:Cévennes, 5:Chizé, 6:Citeaux, 7:Fontainebleau, 8:Landes de Gascogne, 9:Lavaux, 10:Mercantour,

115   11:Orléans, 12:Rambouillet, 13:Rebisclou, 14:Rhue, 15:Taillis.A, 16:Taillis.B, 17:Tronçais, 18:Vieilles

116   Forêts des Pyrénées, 19:Vosges

117

118   2.1. Rapid forest habitat assessment

119   All the stands were characterized by the same observer on a 1-ha circular plot centered on the

120   sampling point where taxonomic data were recorded. The observers followed the protocol for the

121   Index of Biodiversity Potential (IBP; Larrieu and Gonin, 2008), which includes attentive observation

122   while crisscrossing the stand. Nine of the ten IBP factors belong to three broad categories: (i) living

123   vegetation: number of native tree-species and number of vertical strata; (ii) deadwood and TreMs:

124   number of large snags, large lying deadwood items, very large trees and living TreM-bearing trees;

125   (iii) associated features: open areas, number of aquatic macrohabitat types and rocky macrohabitat

126   types. In addition, we replaced the broad IBP variable "*Number of TreM-bearing trees*" by its seven

127   constituting variables *(Table 1);* these variables were used only for relationships between habitat

128   variables and species richness. In all then, a total of 16 compositional and structural stand

129   characteristics (Table 1) were simultaneously recorded on site.

130   Ancientness is also taken into account by the IBP protocol as an additional factor since recent and

131   ancient forests show significant differences in biodiversity (Assman 1999; Gossner et al. 2008; Hermy

132   et al. 1999; Diedhiou et al. 2009). In France, a military survey map showing land use over a large part

133   of the territory (called "Etat Major") was published in the mid-19th century.; Current forests already

134   indicated on this map are considered likely to have never been cleared or replaced with another land

135   use (Dupouey et al. 2002). Ancientness was post-recorded at the office.

136   Finally, we recorded four other covariables: biogeographic domain, location of forested area, altitude

137   and dominant tree-species (Table 1). Hereafter, the term "habitat variables" refers to the IBP

138   constituting variables, while "environmental variables" refers to the total pool of both IBP

139   constituting variables and the four covariables mentioned above.

140   Since the aim of this study was to assess the potential of routine variables as robust habitat

141   surrogates for certain taxa, and not to assess the relevance of the IBP index per se, we did not test

142   the IBP scoring system.

143

144

Table 1. Stand-characterizing habitat variables and covariables; values are at the 1ha-plot scale; d=diameter, L=length; SE=standard error; in italics: variable
derived from a map or computed

Broad categories	Type of variable	IBP's factor number	Variable (Variable number)	Definition	Median	Mean (SD)	Value range (min-max)
Covariables	Covariables		site	Forested area			
			domain	Biogeographic domain: Atlantic or Continental			
			alt	Bioclimatic level: lowlands (plain and hilly levels) or highlands (montane and lower-subalpine levels)			
			broadconif	Tree-species dominance: Broadleaved- (broad), conifer- (conif) dominated or mixed (mixed) stands			
Vegetation	Diversity of tree-species	1	nb.ts (1)	Number of autochthonous tree-species (dead and living trees)	5	5.17 (2.26)	0-12
	Vertical structure of vegetation	2	nb.strata (2)	Number of vertical strata with cover >10% (max=4 ; field cover layer, 0.5-7m, 7-20m, >20m)	4	3.70 (0.52)	2-4
Deadwood and Tree-related microhabitats (TReMs)	Deadwood	3	nb.snags (3)	Number of large snags (d>37,5cm and L≥1m)	1	2.69 (4.65)	0-31
		4	nb.logs (4)	Number of large lying deadwood items (d>37,5cm et L≥1m)	1	4.67 (8.41)	0-57
	Very large trees	5	nb.vlt (5)	Number of very large trees (d>67,5cm)	2	6.54 (9.37)	0-58
	TReM-bearing trees		nb.cav (6)	Number of living cavity-bearing trees: woodpecker breeding and	4	6.80 (12.31)	0-161

6

				feeding holes, root buttress concavities, with an entrance above 3 cm in width; rot-holes with an entrance above 10 cm in width			
			nb.crack (7)	Number of trees with living cracks (or peeling bark forming a shelter)	0	0.31 (0.73)	0-9
			nb.sap (8)	Number of trees with sap-runs > 10 cm in length	0	0.25 (0.62)	0-4
			nb.unbark (9)	Number of living trees with missing-bark (surface > 600 cm²); sapwood is slightly altered	1	2.36 (3.64)	0-37
			nb.fun (10)	Number of fungus-bearing trees: at least one fruiting body of a polypore	0	0.64 (1.27)	0-10
			nb.pdw (11)	Number of trees with crown deadwood (large dead branches > 20 cm in diameter and > 1 m in length, crown deadwood volume > 20% of the total crown wood volume)	2	4.57 (6.19)	0-41
			nb.epiph (12)	Number of living epiphyte-bearing trees: more than 30% of the trunk surface is covered by ivy or liana	1	3.73 (5.90)	0-30
		6	nb.trem (13)	Number of living trees bearing at least one tree-related microhabitat. Trees with more than one microhabitat of the same type were counted only once, but trees bearing more than one microhabitat type were counted once for each microhabitat type	15	16.13 (14.66)	0-160
			div.trem	*Number of tree-related microhabitat types observed (among a list of 7 types)*	4	3.43 (1.84)	0-7
Associated features	Openness	7	open (14)	Open areas (clearings, edges and areas with very little canopy cover) with a well-developed field layer	3	15.17 (27.81)	0-100

			composed of flowering plants (%)			
Associated macrohabitats	8	nb.aqua (15)	Number of aquatic macrohabitat types (among spring, stream, backwater, pond, lake, bog, non-forested marshes)	0	0.35 (0.67)	0-4
	9	nb.rock (16)	Number of rocky macrohabitat types (among cliff, stable or unstable scree, large boulders, slab and other rock outcrops, cave)	0	0.41 (0.84)	0-4
Ancientness	*10*	*ancient (17)*	*The forest is present on the historic "Etat Major" map (19th century)*	-	-	-

147

148   2.2. Taxonomic data

149   Our study targets nine taxa that are widespread in forest ecosystems covering, *a priori*, a wide range

150   of habitat requirements. Four taxa were intrinsically associated with forests, trees, woody substrates

151   or forest-buffered climatic conditions: corticolous lichens, corticolous or saproxylic bryophytes,

152   polypores and saproxylic beetles. Five other taxa– namely ground beetles, hoverflies, birds, bats and

153   vascular plants - had a more heterogeneous ecology. Based on Coulon et al. (2000), Speight et al.

154   (2015), Cramp et al. (1980-94) Arthur and Lemaire (2009) and Rameau et al. (1989, 1999),

155   respectively, we singled out forest specialist subgroups in the assemblages of these five taxa. We

156   defined the subgroups as follows: (i) the forest ground beetle subgroup includes species that are

157   mainly observed in forest ecosystems; (ii) the forest bird subgroup includes species that are mainly

158   observed in forest ecosystems, including tree cavity-dwellers; (iii) the forest bat subgroup includes

159   species using cavities or peeling-barks for resting or breeding; (iv) the forest vascular plant subgroup

160   includes species that are able to grow under closed canopy. Ultimately, we gathered data on one to

161   seven taxa per plot (Table A3) for a total of 14 taxonomic variables (i.e. 9 full groups plus 5

162   subgroups). (Table A4). Sampling procedures are specified in Table A1.

163

164   2.3. Data analyses

165   All the analyses were performed at the plot level. Since several taxa were recorded for

166   presence/absence only (e.g. polypore, bats, bryophytes, lichens), we did not use abundance values in

167   the analyses.

168   2.3.1. Compositional analysis

169   First, we explored the congruence between the between-plot dissimilarity matrix based on pooled

170   habitat variables (see the set of metrics in Table 1) and the between-plot dissimilarity matrix based

171   on species composition (for each of the nine taxa). To do so, we performed a Procrustes rotation on

172   non-metric multi-dimensional scaling (NMDS) ordinations (Peres-Neto and Jackson 2001) of the Bray-

173   Curtis dissimilarity matrix for habitat variables and the Jaccard dissimilarity matrix for species

174   occurrence data. Permutation tests associated to the Procrustes method (*protest* function, R-package

175   *Vegan*, with the m² Procrustes statistic; number of runs=1,000) revealed the non-randomness of the

176   congruence in fit between multivariate data tables. In order to account for the nested structure of

177   our dataset, permutations were conditioned upon forested area, which was a stratifying variable.

178   Next, we performed a Canonical Analysis of Principal Coordinates (CAP, Anderson and Willis 2003;

179   *capscale* function, R-package *Vegan*) to investigate the effects of each habitat feature on variations in

180   species composition for each taxonomic assemblage. Inertia was partitioned from Jaccard's distance

181   matrices (*vegdist* function, R-package *Vegan*) on all explanatory habitat variables, since co-linearity

182   among predictor variables is not a problem in CAP (Anderson and Willis 2003). After partialling out

183   the geographical effect (i.e. forested area), both in the full CAP combining all the habitat variables

184   and in the individual CAPs performed for each habitat variable, we calculated the proportion of

185   inertia cumulatively explained by all the habitat variables, the relative total contribution (intrinsic +

186   co-explained) of each habitat variable to the total inertia and the statistical significance of this

187   contribution (by means of permutation tests - 999 runs).

188

189   2.3.2. Species richness analysis

190   We used multi-model averaged estimates (Burnham and Anderson 2002) to determine the

191   relationship between each of the 14 taxonomic variables for species richness and each of the

192   environmental variables. For each response variable (count data), we generated Poisson Generalized

193   Linear Mixed Models (GLMM, *glmer* function, R-package *lme4*). The mixed models enabled us to

194   include forested area as a random variable. Since co-linearity among predictor variables may lead to

195   unreliable parameter estimates, we followed the strategy suggested by Zuur et al. (2010) to address

196   the multicolinearity problem before model averaging. First, we sequentially dropped the covariate

197   with the highest variance inflation factor (VIF; *vif.mer* function from Frank 2011), then recalculated

198   the VIF; we repeated this process until all VIFs were below the cutoff value of 3 suggested by Zuur et

199   al. (2010). Then, we generated models with all the combinations of the remaining variables and

200   calculated the differences in the Akaike information criterion (AICc, Burnham and Anderson 2002)

201   scores between each model and the null model (dredge function, R-package MuMIn). We also

202   calculated the Akaike weights for each model (model.avg function, R-package MuMIn). Finally, we

203   selected the best two-variable models. Since our aim was to highlight habitat variables as bio-

204   indicators and not to explain taxonomic communities, we did not account for a priori ecological links

205   between the taxon and the habitat variables.

206   Furthermore, we checked the significant relationships (at $p<0.01$) between habitat variables and

207   species richness in the GLMM for thresholds. Threshold values were calculated by recursive

208   partitioning and derived from estimates of breakpoints by means of maximally selected two-sample

209   statistics (Hothorn and Hornik 2006; *ctree* function, R-package *party*). This method provides a

210   conditional inference tree with p-values for one or more critical thresholds. When using the *ctree*

211   function, the model is constrained and does not allow any co-variables or random effects to be taken

212   into account. To deal with this issue, we kept only the most significant results: only primary nodes

213   with highly significant (p < 0.001) thresholds were selected, and only if the number of plots was

214   greater than 30 on either side of the threshold. Then, 95% confidence intervals (bootstrap percentile

215   interval) were calculated for all the selected thresholds, based on 1,000 bootstrap samples (*boot.ci*

216   function, R-package *boot*).

217   In order to standardize sampling effort and to account for missing data for saproxylic beetles, ground

218   beetles and hoverflies (traps destroyed by animals, wind, rain or humans), we used the log of a

219   corrected factor based on the number of undisturbed sampling months as an offset in our models.

220   For vascular plants, we considered the data to be comparable whatever the area sampled (ranging

221   from 600 to 1018 m² since (i) the observers took care to maintain homogeneous local conditions

222   (phytosociological-type sampling), (ii) in forest types similar to those we sampled, Archaux et al.

223   (2007) highlighted samplings set up on areas above 400 m² are comparable, and (iii) the sampled

224   surface area was constant in each forested area (used as a grouping variable in the models). Fungi

225   were sampled along a gradient of one to three years, with one to three runs per year; we therefore

226   only retained polypore records in our analysis, since their sporophores are long-lasting. Bird data was

227   recorded inside 25, 100, and outside 100 m-radius areas; since environmental variables were

228   recorded on 56 m-radius plots (i.e. 1-ha plots), only bird data recorded inside a 25 m-radius area

229   were retained (see Table A1 for details).

230

231   **3. Results**

232   3.1. Variations in species composition

233   Habitat variations significantly (p<0.01) reflected variations in species composition for vascular plants

234   and saproxylic beetles, and to a lesser level of significance (p<0.05) for polypores, bats and lichens.

235   However, they did not reflect variations in species composition for ground beetles, birds, bryophytes

236   or hoverflies (Table 2).

237

238   Table 2. Procrustes analysis of the inter-plot congruence in fit between species and habitat
239   dissimilarity matrices; permutation tests were conditioned on forested area; Procrustes test
240   significance: **: 0.001<p<0.01; *: 0.01<p<0.05; ns=non-significant. Procrustes metrics = symmetric
241   Procrustes sum of squares between matrices (m12), derived by the Procrustes rotation method in
242   correlation-like statistics

Taxon	Procrustes metrics	p-value
Vascular plants	0.623	**
Lichens	0.807	*
Bryophytes	0.786	ns

Polypores	0.902	*
Saproxylic beetles	0.855	**
Ground beetles	0.831	ns
Hoverflies	0.929	ns
Birds	0.924	ns
Bats	0.940	*

243

244

245 3.2. Habitat variables as indicators of biodiversity

246 3.2.1. Relationships between habitat variables and species composition for full taxa

247 Individual habitat variables did not contribute very much (from 0.46 to 58.03%) to variations in

248 species composition (total inertia) as estimated by CAP (Table A4). However, when we tested the

249 whole set of nine recorded variables (or 10 if ancientness could be determined), excluding the

250 "forested area" random effect, contributions ranged from 6.05% (for saproxylic beetles) to 88.33% of

251 the total inertia (for lichens) (Table A4, last column).

252 We found numerous significant relationships between habitat variables and species composition (Fig.

253 2; details in Table A4). Vascular plants, saproxylic beetles and polypores showed the largest

254 proportion of significant relationships tested (100%, 100% and 80%, respectively, at $p<0.05$). On the

255 other hand, we did not find any significant relationships between habitat variables and bats (Table

256 A4). However, the set of habitat variables contributed to 9.5% of bat inertia.

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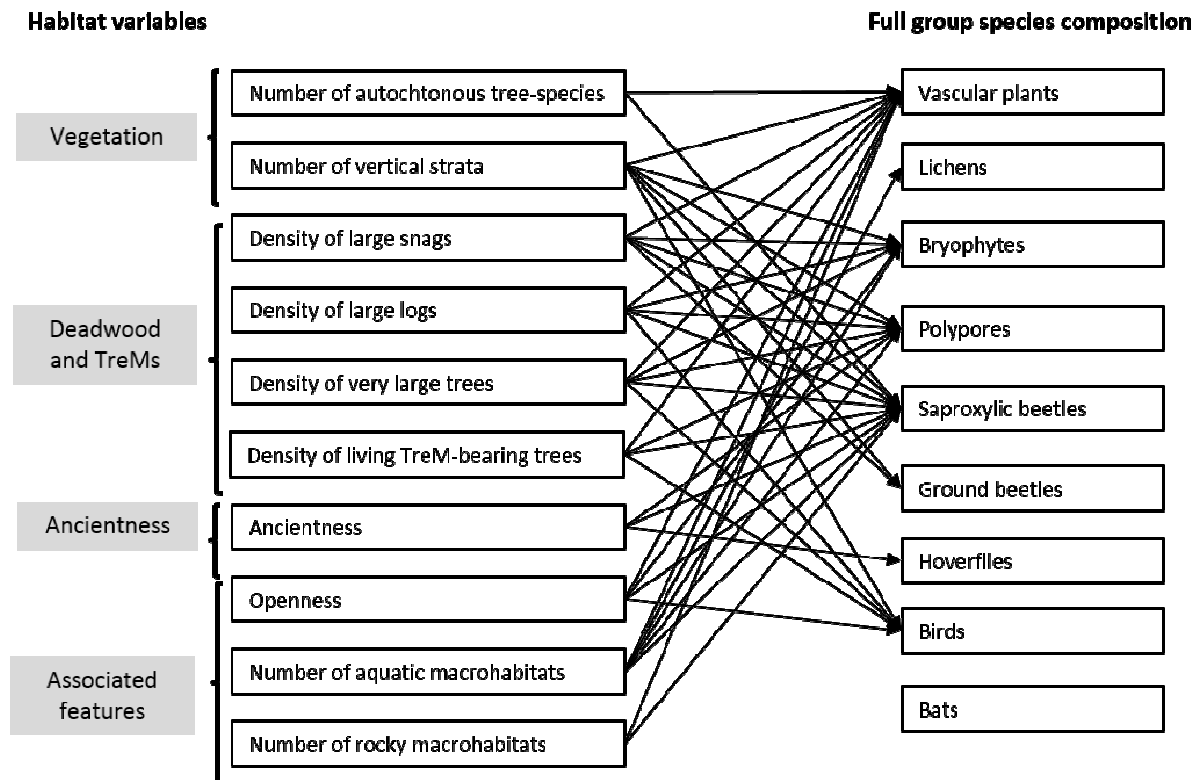
Figure 2. Relationships between the ten habitat variables (left) and inter-plot variation in species composition (right) for nine taxa (full groups) at the plot scale; only significant relationships at p<0.01 are shown (solid arrows); TreMs: tree-related microhabitats; ancientness was tested for only saproxylic beetles, ground beetles, hoverflies and polypores since sampling was unbalanced for the other taxa

267

3.2.2. Relationships between habitat variables and species richness for full taxa

At the plot scale, the 10 IBPvariables taken separately had fewer significant effects on species richness than on species composition (n=31 and n=49, respectively at p<0.05; Table A4 for species composition & A5 for species richness). However, most of the habitat variables showed significant relationships with the species richness of at least one of the taxa (at p<0.01; Fig. 3). We observed more positive relationships than negative ones (n=23 and n=7, respectively, at p<0.05). Only vascular plants, bryophytes and saproxylic beetles showed significant relationships with the covariables. Whenthe whole set of habitat variables was considered (N=17), saproxylic beetles, bats, and hoverflies showed the largest number of significant relationships (n=10, 7 and 7, respectively, at p<0.05), while lichens showed only two. The best determining habitat variables (at p<0.001) on species richness were (Table A5): (i) the number of vertical strata on ground beetles (-) and hoverflies (+); (ii) the density of large snags on bryophytes (+); (iii) the density of large logs on bryophytes (+);

280   (iv) the density of trees with crown deadwood on hoverflies (-); (v) the density of polypore-bearing

281   trees on polypores (+); (vi) the density of trees with missing bark on both polypores(+) and hoverflies

282   (+); (vii) the density of cracks on saproxylic beetles (+); (viii) openness on both vascular plants (+) and

283   saproxylic beetles (+); (ix) the number of aquatic macrohabitats on vascular plants (+), polypores (+)

284   and saproxylic beetles (+); and (x) the number of rocky macrohabitats on saproxylic beetles (+).

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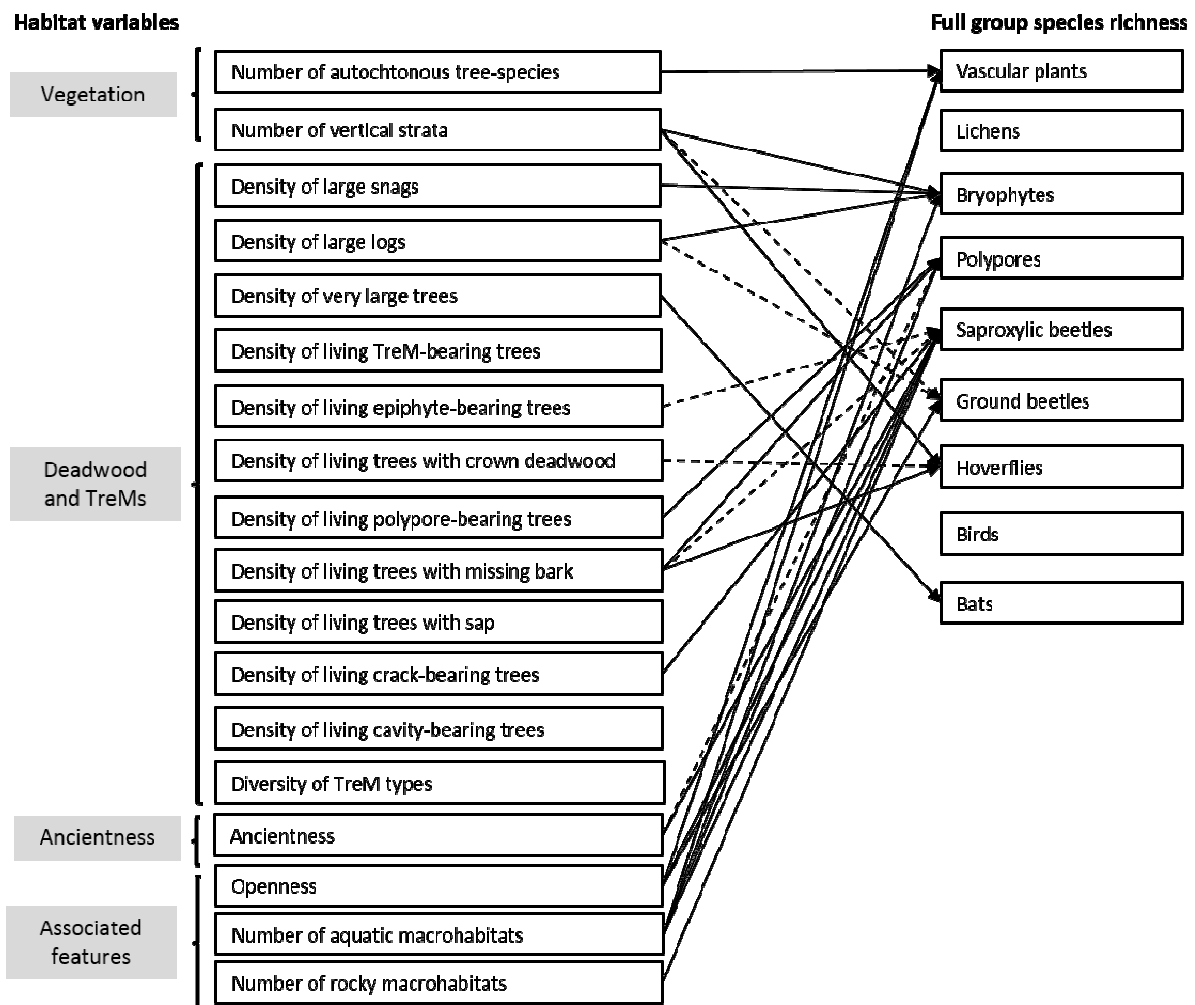
287   Figure 3. Relationships at the plot scale between 18 habitat variables and the species richness of 9
288   taxa (full groups); significant relationships at p<0.01 are shown by solid or dashed arrows for positive
289   and negative relationships, respectively; TreMs: tree-related microhabitats; ancientness was tested
290   only for saproxylic beetles, ground beetles, hoverflies and polypores since sampling was unbalanced
291   for the other taxa

292

293   Furthermore, the species richness of saproxylic beetles at the plot scale was positively affected by

294   increasing altitude, non-Atlantic geographical location and dominance of broadleaves (Table A5).

295   Increasing altitude also had a positive effect on the species richness of bryophytes while it had a

296   negative effect on that of vascular plants.

297

298   The two most common habitat variables in the best two-variable models for species richness were

299   number of tree-species (n=5) and number of aquatic macrohabitats (n=5) (Table 3). The best model

300   for saproxylic beetle diversity included only covariables.

301

302   Table 3. Best models (GLMM; max. 2 terms) for the alpha-diversity of nine full taxa and four forest

303   subgroups; forested area was a random variable; see Table 1 for abbreviations

Taxon	Best model (AICc)	AIC null model
Vascular plants	alt + nb.aqua (1262.50)	1296
Forest vascular plants	nb.aqua + nb.ts (961.8)	1014.4
Lichens	nb.roch + nb.strata (165.87)	168.91
Bryophytes	nb.aqua + nb.logs (819.20)	843.41
Polypores	nb.aqua + nb.fungi (914.03)	946.97
Saproxylic beetles	decidconif + domain (3173.50)	3305.5
Ground beetles	nb.logs+nb.strata (907)	939.60
Forest ground beetles	nb.aqua+nb.fun (914.03)	1188.90
Hoverflies	alt + nb.pdw (1161.10)	1188.90
Forest hoverflies	nb.ts+ nb.sap (787.55)	798.85
Birds	nb.ts+ nb.vlt (672.88)	681.21
Forest birds	nb.ts+nb.vlt (666.55)	675.05
Bats	nb.ts +nb.vlt (480.92)	488.17
Forest bats	nb.snags +nb.roch (405.25)	406.44

304

305

306   Briefly, the habitat variables with the highest number of significant ($p<0.05$) effects on taxa (full

307   groups) were: (i) **for species composition**, the density of large snags (n=8), the density of large logs

308   (n=6), the density of very large trees (n=6), the number of vertical strata (n=6), the number of aquatic

309   macrohabitats (n=6), the density of TreM-bearing trees (n=5), and openness (n=5); and (ii) **for species**

310   **richness**, the number of vertical strata (n=5), the number of aquatic macrohabitats (n=5) and the

311   density of large logs (n=4).

312

313   Except for lichens, hoverflies, birds and bats, we found at least one significant ($p<0.01$) habitat driver

314   for every taxon, **both for species richness and composition** (Fig. A1; details in Tables A4 and A5).

315   Among these significant habitat drivers, only five affected two or more taxa: (i) the number of

316   vertical strata for bryophytes and ground beetles, (ii) the number of large snags for bryophytes and

317   saproxylic beetles, (iii) ancientness for polypores and saproxylic beetles, (iv) openness for vascular

318   plants and saproxylic beetles, and (v) the number of aquatic macrohabitat types for vascular plants,

319   bryophytes, polypores and saproxylic beetles.

320

321

322   3.2.3. Relationships between habitat variables and forest species richness and composition

323   Unexpectedly, most of the forest subgroups showed fewer significant relationships with habitat

324   variables than did the full-groups. This was true for both species richness and composition (Fig. A2

325   for species composition, Fig. A3 and Table A5 for species richness). Only forest vascular plant species

326   composition showed a number of significant relationships similar to the corresponding full group.

327   Furthermore, as with the full taxonomic groups, none of the habitat variables significantly affected all

328   the forest groups combined, either in terms of species richness or species composition. The density

329   of large logs and openness had a significant effect on the species composition of three out of the four

330   forest groups (namely forest vascular plants, forest birds and forest ground beetles). Only forest birds

331   showed the same best 2-term models for species richness as the related full group (Table 3). We did

332   not reveal any clear driver for forest bats for either species richness or species composition.

333

334   3.3.2. Significant thresholds for the relationships between habitat variables and variations in species

335   richness

336   We found seven significant (p<0.001) threshold values at the 1ha-plot scale for the following positive

337   (+) or negative (-) significant (p<0.01) relationships between habitat variables and the species

338   richness of the 14 studied taxonomic groups (Table 4 and Fig. A4, A5, A6, A7, A8 and A9). (i) Vascular

339   plants gained 50% in species richness above four autochtonous tree species. (ii) Forest vascular plant

340   species richness gained 77% above four autochtonous tree species. (iii) Bryophyte species richness

341   gained 15% above three large logs. (iv) Polypore species richness gained 340% above one aquatic

342   macrohabitat. (v) Forest ground beetle species richness gained 40% above one polypore-bearing

343   tree. (vi) Forest ground beetle species richness gained 75% above one tree with missing bark. Finally,

344   (vii) Ground beetle species richness lost 69% above three strata.

345

346

347 Table 4. Significant thresholds (*p*<0.001) in positive relationships between habitat variables and
348 taxon species richness at the 1ha-plot scale (see Table A5); Magnitude: relative increase/decrease
349 between median values below and above the threshold; CI 95: confidence interval at 95% (5,000
350 bootstrap samples); d=diameter, dbh=diameter at breast height, TreM=tree-related microhabitat

Variable	Taxon	Thresholds [CI 95]	Medians below/above the threshold (nb of plots)	Magnitude	Synthesis for an integrated management strategy
Number of autochtonous tree species	Vascular plants	4 [4-6]	26(n=47)/39(n=100)	+50%	N≥4: significant increase in species richness for vascular plants
Number of autochtonous tree species	Forest vascular plants	4 [4-5]	13 (n=47) / 23 (n=100)	+77%	N≥4: significant increase in species richness for forest vascular plants
Density of large logs (d≥40 cm)	Bryophytes	3 [2-12]	13(n=59)/15(n=83)	+15%	N≥3: significant increase in species richness for bryophytes
Number of types of aquatic habitats	Polypores	1 [0-1]	5 (n=126)/17 (n=31)	+340%	N≥1: significant increase in species richness for polypores
Density of living polypore-bearing trees	Forest ground beetles	1 [0-1]	5 (n=97)/7 (n=76)	+40%	N≥1: significant increase in species richness for forest ground beetles
Density of living trees with missing bark	Forest ground beetles	1 [0-1]	4 (n=41)/7 (n=132)	+75%	N≥1: significant increase in species richness for forest ground beetles
Number of vegetation strata	Ground beetles	3 [2-3]	26 (n=43)/8 (n=127)	-69%	N≥3: significant decrease in species richness for ground beetles

351

352

353 **4. Discussion**

354

355 Among the numerous results relating the species composition and diversity of the studied taxonomic
356 groups to the selected environmental variables, most were expected. However, a few were
357 surprising in ecological terms. For example, we found positive relationships between saproxylic
358 beetle species richness and the number of aquatic and rocky macrohabitats. However, aquatic and
359 rocky macrohabitats often result in a higher degree of stand openness when they occur, and we
360 show that openness favors higher saproxylic beetle species richness. The negative relationship
361 between hoverfly species richness and the density of trees with crown deadwood was equally
362 surprising since several hoverfly species do use crown deadwood during their larval stage (Speight et

17

363 al. 2015). These results may be due to the systematic selection of the explanatory variables we

364 applied to our models, which we did not base on ecological hypotheses; or by indirect effects related

365 to more efficient sampling of hoverflies with our flight interception traps in open stands than under a

366 dense canopy. Higher hoverfly species richness has been observed in open stands (Gittings et al.

367 2006). Indeed, more open stands provide the species-rich herb layer adult hoverflies need as a

368 source of pollen and nectar (Fayt et al. 2006), although several forest species are saproxylic at the

369 larval stage and often depend on various saproxylic substrates in mature closed-canopy stands (see

370 also Herrault et al. 2016).

371

372 4.1. Using species composition vs species richness to highlight habitat surrogates

373 Most of the previous studies dealing with the relationships between habitat variables and taxa have

374 focused on species richness alone (Gao et al. 2015). However, we found more significant

375 relationships between habitat variables and species composition than between habitat variables and

376 species richness. Only 16% of the tested relationships were significant (at p<0.01) for both species

377 richness and composition. This confirms that species composition is relevant when selecting

378 biodiversity surrogates and investigating the relationships between biodiversity and habitat

379 variables. Indeed, species composition provides results complementary to those obtained through a

380 species-richness approach for cross-taxon congruence (Larrieu et al. 2018; Jokela et al. 2018).

381 However, species composition is slightly more difficult to interpret than species richness, especially in

382 terms of the magnitude of the relationship. Alternative approaches, not pursued here, include using

383 more precise ecological subgroups (Barbier et al. 2009; Gosselin 2012; Zilliox and Gosselin 2014) or

384 performing analyses at the species level (Okland et al. 1996; Bouget et al. 2014b). However, the

385 practical comprehensive life-trait databases required by such approaches are available for very few

386 taxa (e.g. Syrph the Net for hoverflies; Speight et al. 2015) and most life-trait descriptions must

387 therefore be collected from a variety of dispersed sources.

388

389 4.2. New insights on relationships between habitat variables and biodiversity

390 Most of the relationships we found between the habitat variables and species richness were positive

391 (77%). However, the number of vertical strata, the density of large logs, the density of trees with

392 missing bark and ancientness showed both positive and negative relationships, depending on the

393 taxon.

394 We found that the density of large logs was a relevant variable for the species richness of corticolous

395 and saproxylic bryophytes, which is partly in line with Söderström (1988a, b), Andersson and

396   Hytteborn (1991) and Sabovljevic et al. (2010) who revealed a positive relationship between log

397   diameter and the frequency of saproxylic bryophytes. We also revealed that the density of large

398   snags was a relevant indicator for the species richness of corticolous and saproxylic bryophytes,

399   although snags had previously been highlighted as a bryophyte-poor substratum (Lõhmus et al. 2007)

400   less crucial than logs for this taxon (Humphrey et al. 2002). Finally, Tönnberg (2001) found no

401   correlation between the local amount of deadwood and the species richness of saproxylic

402   bryophytes. We therefore conclude that focusing on any large deadwood items (both logs and snags)

403   may be a simpler yet efficient way to check for bryophyte diversity with a view to conservation.

404   Ancientness is known to influence assemblage composition for true bugs (Gossner et al. 2008),

405   ectomycorhizic fungi (Diedhiou et al. 2009), soil fauna (Janssen et al. 2018) and - among the taxa in

406   this study - vascular plants (e.g. Hermy and Verheyen 2007; Dupouey et al. 2002), ground beetles

407   (Assmann 1999), saproxylic beetles (Brin et al. 2016; Janssen et al. 2016, 2017), hoverflies (Herrault

408   et al. 2015), bryophytes and epiphytic lichens (Rose 1993; Fritz et al. 2008; Janssen et al. 2019).

409   Unfortunately, we were not able to test for an ancientness effect on the species composition of

410   bryophytes, lichens, bats, birds and vascular plants since our sampling design was very unbalanced.

411   However, like Herrault et al. (2015), we found that ancientness was a key feature for species

412   composition in hoverflies for the full group (but not for forest-specialists alone). Contrary to Assmann

413   (1999), we did not find that ancientness influenced ground beetle assemblages. Finally, we found

414   that ancientness is relevant for the species richness of polypores, though unexpectedly, the

415   relationship was negative. To our knowledge, this is an original result. However, it should be noted

416   that our sampling design had a high proportion of young stands hosting pioneer tree species, which

417   can quickly provide saproxylic substrates due to their short lifespan, thus promoting high polypore

418   diversity. Although we found lower polypore species richness in ancient forests, the highly significant

419   relationship between ancientness and the composition of polypore assemblages showed that this

420   factor does play a role in fungus conservation by promoting specific species.

421

422   The variable "number of autochthonous tree-species" occurred in 36% of our best models for species

423   richness. This relationship was expected for vascular plants since i) species richness for non-woody

424   plants, shrubs and trees are all positively influenced by the nutrient richness of the soil (e.g. Rameau

425   et al. 1999) and ii) both tree seedlings and small saplings are commonly included in the vascular plant

426   sample. A similar relationship was also expected for forest hoverflies, bats and birds since a stand

427   encompassing a mix of tree species provides a wider range of both feeding resources for hoverfly

428   larvae and resting and breeding microsites for bats and birds than does a pure stand. Mixed stands

429 better match the requirements of different taxa (e.g. Cramp et al. 1980; Arthur and Lemaire 2009;

430 Speight et al. 2015).

431 The variable "number of aquatic macrohabitats" occurred in 36% of our best models for species

432 richness and was relevant for the species composition of six out of nine taxa (full groups). This type

433 of habitat is often considered specific to aquatic taxa only, whereas our findings suggest that aquatic

434 macrohabitats could be more widely used as an indirect indicator of wet conditions in general.

435

436 4.3. Most of the forest taxonomic subgroups showed weaker relationships with habitat variables than

437   did full-groups

438 We built forest subgroups for bats, birds, hoverflies, ground beetles and vascular plants since (i)

439 forest-specialist species are often targeted for conservation by forest managers who use an

440 integrated approach, and (ii) we expected stronger relationships than for the full groups since the

441 latter encompass species ranging beyond forest conditions. However, we found more numerous

442 significant relationships between full groups and habitat variables than we did for forest subgroups

443 alone. Several reasons may explain this result. First, the life-trait databases or the variables we used

444 to build our forest subgroups may not have been completely relevant. For example, dwelling in

445 cavities or under peeling bark may not be the most relevant feature for forest-specialist bats, very

446 few of which are strict tree-roosters; most also make use of similar microhabitats provided, for

447 instance, by buildings (Arthur and Lemaire 2009). Secondly, forest specialists may mainly depend on

448 habitat variables we either did not record or recorded too broadly (i.e. our variables may not have

449 focused on features specific enough to definitely select the forest specialist), or which we did not

450 record at the most appropriate spatial scale. Thirdly, taxa such as hoverflies are multi-habitat users,

451 i.e. saproxylic species need deadwood substrates while all adults need flower resources (Speight et

452 al. 2015). This means that the presence of saproxylic hoverflies is mostly linked to the co-occurrence

453 of both deadwood and flowering plants in the same stand. Another explanation might be that only a

454 part of the habitat feature is included in the IBP variables; for example, only deadwood items over 40

455 cm in diameter are recorded and, although these large items are crucial for biodiversity (e.g. Gossner

456 et al. 2013), most saproxylic species require a wider range of diameters. Finally, the relationship with

457 the non-forest species in the full group may have actually been stronger than with the forest

458 specialists.

459 Stronger relationships between habitat variables and non-forest vascular plants than with forest

460 vascular plants have already been found (Barbier et al. 2009; mostly Zilliox and Gosselin 2014).

461   Among bryophytes, forest-specialists do seem to have stronger relationships with forest habitat

462   variables than do the other species in the taxon (Gosselin et al. 2014). Yet a practical life-trait

463   database relevant for France is lacking since the databases available in Europe to date are limited to

464   the UK (Hill 2007) and Germany (Schmidt 2013).

465

466   4.4 From ecological results to forest management guidelines: providing thresholds

467   When we analyzed our species richness models in terms of the magnitude of the relationships (as in

468   e.g. Barbier et al. 2009 and Zilliox & Gosselin 2014), we found rather strong relationships between

469   habitat variables and species composition, and weak (though sometimes significant) relationships

470   between habitat variables and species richness, with one notable exception (the relationship

471   between the number of strata and hoverfly species richness). Yet, threshold analyses revealed some

472   strong, non-linear relationships between certain habitat variables and species richness for some taxa.

473   Forest management encompasses a wide range of technical, economic and environmental aspects,

474   and covers a wide array of disciplines. Therefore, managers are often faced with complex trade-offs.

475   Simple and efficient guidelines can help them better integrate biodiversity issues in both

476   management plans and technical procedures. Critical thresholds for taxon response to habitat

477   variations are among the simplest tools (Müller and Bütler 2010). Significant thresholds at the stand

478   scale for crucial deadwood amounts (Müller and Bütler 2010; Gossner et al. 2013), optimum range of

479   canopy openness, proportion of deciduous trees and optimum stand age (Moning and Müller 2008,

480   2009) have already been published for snails, birds, saproxylic beetles, fungi, mosses and lichens. In

481   our case, we did not record stand age since most of the stands we sampled were uneven-aged. For

482   deadwood, we used a complementary approach. First, we chose density rather than total volume for

483   deadwood items since assessing density does not require measurements or calculations and is easier

484   for occasional forest managers (e.g. owners of small woodlands) to use. Second, we focused on

485   particular features such as large deadwood items or very large trees, which are typically rare in

486   managed forests (Bauhus et al. 2009, Paillet et al. 2015) yet are relevant for saproxylic beetles

487   (Gossner et al. 2013), fungi or forest bryophytes (Gosselin et al. 2014, 2017), among others. We

488   provide seven significant thresholds. Among them, five thresholds seem to be related to ecological

489   requirements: the number of autochtonous tree species for vascular plants (both full- and forest

490   subgroup; positive relationship; see discussion above), the density of large logs for bryophytes (as

491   crucial substrates; positive relationship), the number of aquatic macrohabitats for polypores (positive

492   relationship; probably because wet conditions favor the growth of fungi), and the number of

493   vegetation strata for ground beetles (negative relationship; ground beetles are mostly heliophilous

494   and mainly associated to non-forest ecosystems). The two others, i.e. the density of living polypore-

495   bearing trees and trees with missing bark for forest ground beetles, are likely to hide correlations

496   with other ecological factors, and this may reduce their relevance in contexts outside the range of

497   forest types we studied.

498

499   Gosselin et al. (2014) showed that using other statistical methods (taking into account random

500   effects, specific probability distribution, spatial autocorrelation and other continuous sigmoid

501   functions) led to larger confidence intervals around thresholds. Furthermore, an ongoing study

502   highlights that variations in threshold values among forest sites (and also the curve pattern) may

503   have an impact on estimations of the magnitude of the relationships (Godeau et al. submitted). As in

504   Gosselin et al. (2014) and Godeau et al. (submitted), the inclusion of non-linear relationships allowed

505   us to detect strong relationships with species richness, while the use of (generalized) linear models

506   only mostly revealed only weak relationships. Further research should therefore focus on properly

507   estimating thresholds and non-linear relationships between habitat variables and biodiversity

508   metrics for a large range of taxa and forest contexts. However, since we used highly demanding

509   criteria and kept only the most significant thresholds, we are confident that our thresholds are

510   relevant for the conservation of the concerned taxa in temperate forests.

511

512   4.5. How to deal with only a few weak relationships between habitat variables and biodiversity

513   The Procrustes approach showed that the ten IBP habitat variables considered together were

514   relevant when assessing variations in species composition for five of the nine taxa studied (56%).

515   Further research should consider variations in functional diversity and use taxon life-traits in order to

516   evaluate whether the variations in species composition are related to functional changes. It would

517   also be relevant to test covariations on key taxa for ecosystem functioning such as soil-dwellers (e.g.

518   Zanella et al 2017). Managers would respond more readily to demands for biodiversity preservation

519   if the changes they implement resulted in better ecosystem functioning.

520

521   This study highlights numerous significant relationships between individual habitat variables and

522   biodiversity and provides practical thresholds for management. However, none of the habitat

523   variable combinations consistently explained the variations in species richness for all the taxa

524   studied. Furthermore, the contribution of the habitat variables to total species composition inertia

525   was relatively low (median=10.4%, mean=15.9, range: 6-88%). The limited explanatory power of our

526   environmental indicators for biodiversity can be linked to several effects. First, nonlinear effects may

527 be at play (Araujo et al. 2003); this is consistent with our findings that threshold non-linear models

528 gave stronger relationships than did generalized linear models for species richness. Second, the

529 suitable niches might not have been fully occupied due to time-lag responses (Cristofoli and Mahy

530 2010; Jackson and Sax 2010). In addition, non-environmental factors may have been predominant

531 biodiversity drivers (Hortal et al. 2009). Finally, our taxonomic samplings could have been

532 incomplete, or other environmental factors not considered in our study could have been involved.

533

534

535 **6. Conclusion and research perspectives**

536 It is relevant in a funds-limited context to consider an indicator in terms of both performance and

537 cost. Environmental indicators are easy to assess during routine management activities and are the

538 cheapest indicators for species richness in Mediterranean ecosystems (Mandelik et al. 2010).

539 Furthermore, recording taxonomic data is time-consuming and costly, even though it is possible to

540 pre-select taxa by optimizing the cost/performance ratio (Gardner et al. 2008; Larrieu et al. 2018).

541 Schamberger (1988) and Noss (1990) believe that monitoring both habitat and taxa is essential in

542 most cases. Landres et al. (1988) also recommend mixing taxonomic and environmental indicators

543 while Ferris and Humphrey (1999) suggest using a combination of several structural and

544 compositional indicators. Composite data sets combining both taxonomic and environmental data

545 have already demonstrated their efficiency and have led to progress in biodiversity protection

546 (Pressey 2004; Cowling et al. 2004). To go further, Vierikko et al. (2010) suggest using a combination

547 of taxonomic, environmental and socio-economic indicators to monitor sustainable forestry goals.

548 According to Duelli and Obrist (2003), an index combining a set of indicators is the best approach.

549 Based on the combined results of this study and those of a companion study assessing cross-taxon

550 congruence patterns and the cost-efficiency of surrogate taxa (Larrieu et al. 2018), we propose the

551 following recommendations to help forest managers promote more biodiversity-friendly forest

552 management: (i) routinely apply a rapid habitat assessment such as the IBP; (ii) use appropriate

553 silvicultural techniques to increase or maintain autochtonous tree diversity and the density of large

554 logs above the thresholds highlighted in this study; (iii) conserve the diversity of aquatic habitats; and

555 (iv) periodically carry out a biodiversity assessment at the forest scale by recording taxonomic data

556 focusing on saproxylic beetles and vascular plants, or on saproxylic beetles, vascular plants and birds

557 (the most cost-efficient associations, according to Larrieu et al. 2018).

558 Due to the wide range of taxa and forest types sampled in this study, we believe our findings and

559 recommendations are relevant at the stand scale for temperate European forests. However, further

560　　research would be welcome since (i) most of our taxonomic data are related to a single sampling

561　　year; ii) habitat variables were only recorded at the stand scale (landscape-level environmental

562　　variables should also be recorded); (iii) only one metric was used to evaluate alpha diversity (i.e.

563　　species richness); (iv) we used presence/absence data to be consistent among the taxa but adding

564　　abundance data could be beneficial; and (v) statistical analyses could be improved (e.g. non-linear

565　　approaches, consideration of more random effects). Research should also consider broader temporal

566　　(Favreau et al. 2006) and spatial scales (Yoccoz et al. 2001, Bouvier et al. 2017) as well as take into

567　　account adjacent habitats and their management, in particular for small woodlands (Tölgyesi et al.

568　　2018). Research should also consider some poorly-known and very diverse taxa, which play a key role

569　　in ecosystem functioning, such as soil fauna, Diptera other than hoverflies, moths, fungi other than

570　　polypores and parasitoid Hymenoptera.

571

572　**Acknowledgements**

583

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