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1 **Assessing the potential of routine stand variables from multi-taxon data as habitat surrogates in**  
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 autochthonous 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

47

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

53

54

## 55 **1. Introduction**

56 Forests are crucial habitats for biodiversity since they support about two-thirds of the world's  
57 terrestrial biodiversity (WCFSD, 1999). In Europe, most forests have been managed for a long time  
58 (Larsson et al. 2001), and this has had a major impact on their biodiversity (e.g. Mitchell and Kirby  
59 1989). The concept of sustainable forest management, which emerged at the 1992 Rio conference on  
60 Environmental Development, requires forest managers to maintain species diversity in managed  
61 areas (FAO 2015). However, taxonomic inventories are time-consuming and involve specialists, and  
62 therefore cannot be easily implemented by forest managers in their daily routine. Having said this,  
63 some quick, easy methods ("rapid habitat assessments") exist to survey key structural elements and  
64 succinctly describe the habitats typical of various forest taxa (Venier and Mackey 1997). Lindenmayer  
65 et al. (2000) suggested using environmental variables as biodiversity indicators. Testing and  
66 validating easy-to-record stand variables that depict species habitats and are relevant as biodiversity  
67 indicators would encourage forest managers to integrate these indicators into their typical working  
68 activities. . Larsson et al. (2001) proposed a list of key compositional, structural and functional  
69 environmental factors for each main European forest type. In the same way, Lindenmayer et al.  
70 (2006) suggested using keystone elements to improve and monitor eco-friendly forest management.  
71 Their focus was mainly on deadwood and tree-related microhabitats (TreMs) (Tews et al. 2004; Kraus  
72 and Krumm 2013). Composite indices, based on large-scale field data available from state forest  
73 inventories, have already been used in habitat assessment protocols (e.g. The Stand-scale Forest  
74 Biodiversity Index, Van Den Meersschaut and Vandekerckhove, 1998; the Austrian Forest Biodiversity  
75 Index, Geburek et al. 2010; The Biotope Value of the Forest Stand, WSL 2001). At the local (i.e. stand)  
76 scale, other indicator lists exist (e.g. Indicators of High Conservation Value Forest, Jennings et al.  
77 2003; the European forest scorecards, Sollander 2000; The Rapid Appraisal of Riparian Condition,  
78 Jansen et al. 2004).

79 Unfortunately, the studies to date have not identified habitat indicators that are fully relevant for all  
80 taxa and all forest contexts (e.g. Bouget et al. 2014a; Van Den Meersschaut and Vandekerckhove  
81 1998), and significant relationships between structural indicators and taxa has clearly been shown in  
82 only a very limited number of cases (Gao et al. 2015). Furthermore, most previous studies have  
83 focused on species richness, while the relationships between indicators and species composition  
84 have been poorly studied (Gao et al. 2015). Finally, Gao et al. (2015) recommended that  
85 environmental variables be further validated for forest ecosystems.

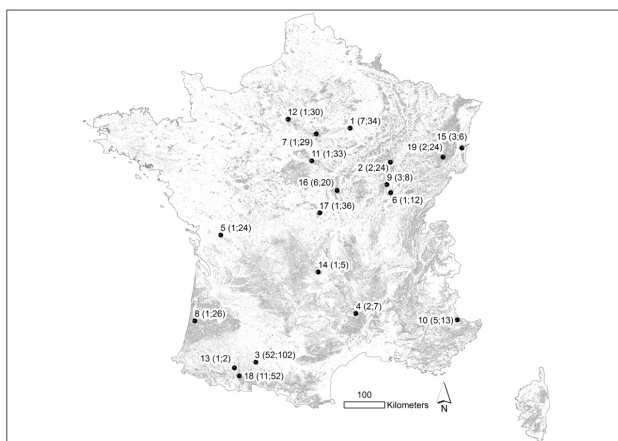
86 We chose to focus on species subgroups such as forest specialists (Gosselin 2012), since they are  
87 often the main targets of forest conservation, and to emphasize the stand scale, since it is the main  
88 operational scale for forest managers (Failing and Gregory 2003). The habitat variables 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.)

110



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:Auvergne, 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-19<sup>th</sup> 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

145 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  
 146 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 domain	Forested area 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

				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 cm <sup>2</sup> ); 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
			<i>div.trem</i>	<i>Number of tree-related microhabitat types observed (among a list of 7 types)</i>	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)	<i>The forest is present on the historic "Etat Major" map (19<sup>th</sup> century)</i>	-	-	-

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  $m^2$  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 multicollinearity 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 m<sup>2</sup>) 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 m<sup>2</sup> 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).

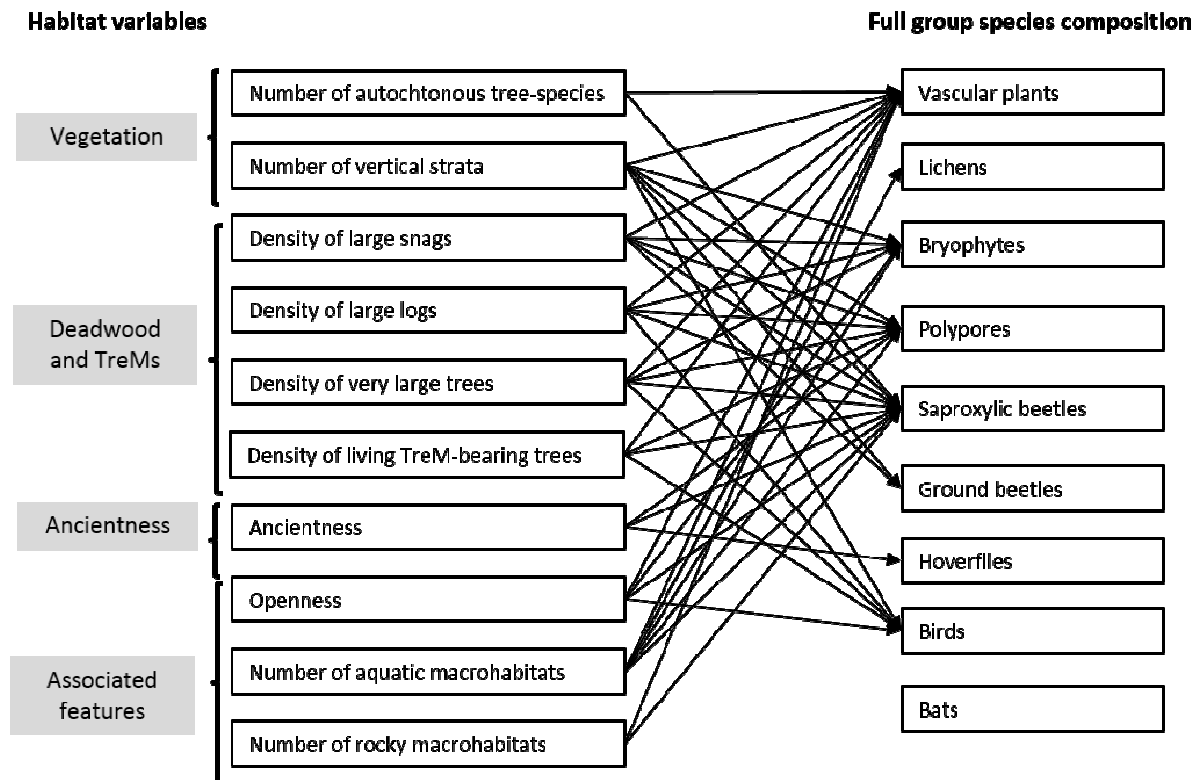
252 We found numerous significant relationships between habitat variables and species composition (Fig.  
 253 2; details in Table A4). Vascular plants, saproxylic beetles and polypores showed the largest  
 254 proportion of significant relationships tested (100%, 100% and 80%, respectively, at  $p < 0.05$ ). 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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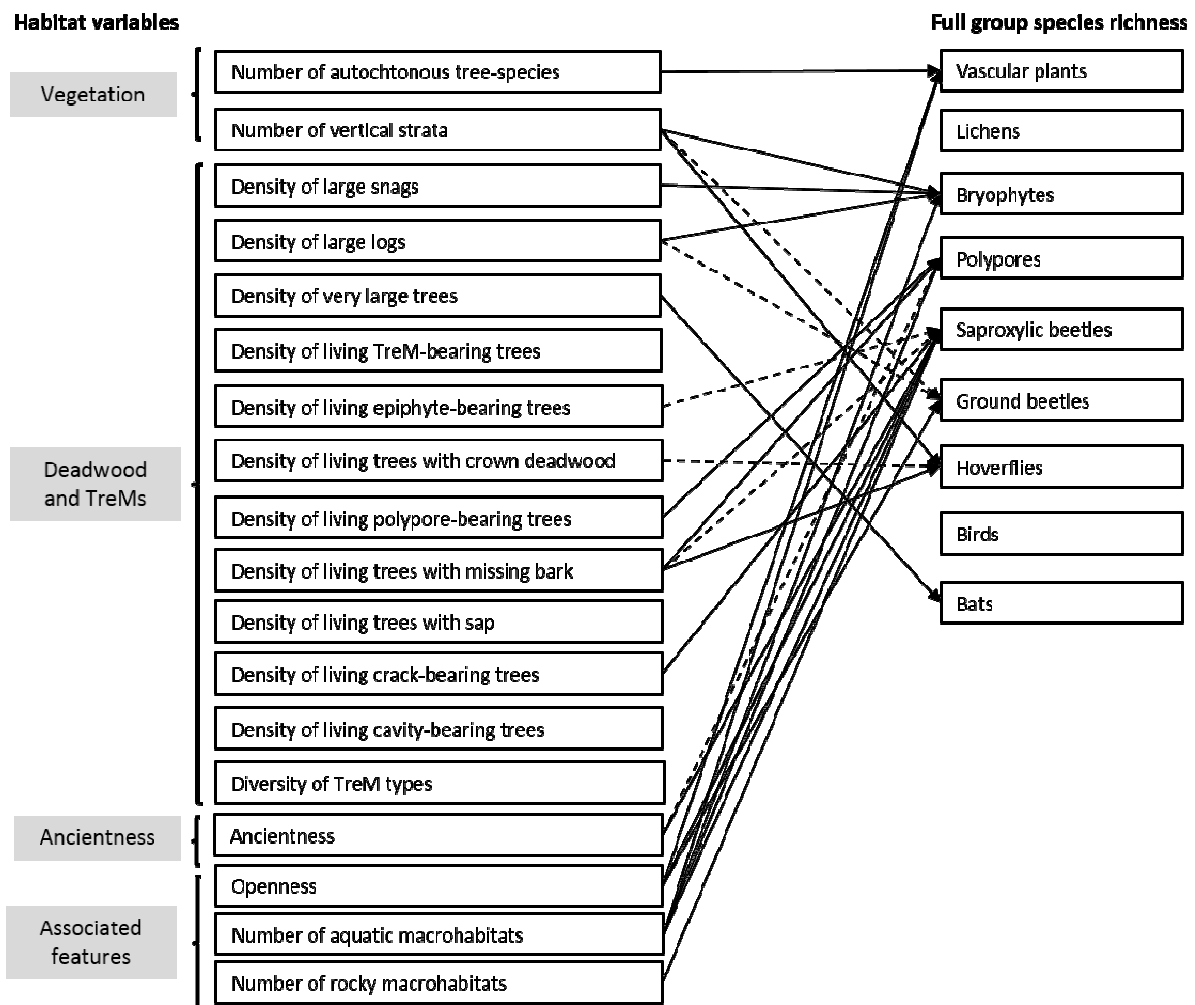
262 Figure 2. Relationships between the ten habitat variables (left) and inter-plot variation in species  
 263 composition (right) for nine taxa (full groups) at the plot scale; only significant relationships at  $p < 0.01$   
 264 are shown (solid arrows); TreMs: tree-related microhabitats; ancientness was tested for only  
 265 saproxylic beetles, ground beetles, hoverflies and polypores since sampling was unbalanced for the  
 266 other taxa

267

### 268 3.2.2. Relationships between habitat variables and species richness for full taxa

269 At the plot scale, the 10 IBP variables taken separately had fewer significant effects on species  
 270 richness than on species composition ( $n=31$  and  $n=49$ , respectively at  $p < 0.05$ ; Table A4 for species  
 271 composition & A5 for species richness). However, most of the habitat variables showed significant  
 272 relationships with the species richness of at least one of the taxa (at  $p < 0.01$ ; Fig. 3). We observed  
 273 more positive relationships than negative ones ( $n=23$  and  $n=7$ , respectively, at  $p < 0.05$ ). Only vascular  
 274 plants, bryophytes and saproxylic beetles showed significant relationships with the covariables.  
 275 When the whole set of habitat variables was considered ( $N=17$ ), saproxylic beetles, bats, and  
 276 hoverflies showed the largest number of significant relationships ( $n=10$ , 7 and 7, respectively, at  
 277  $p < 0.05$ ), while lichens showed only two. The best determining habitat variables (at  $p < 0.001$ ) on  
 278 species richness were (Table A5): (i) the number of vertical strata on ground beetles (-) and hoverflies  
 279 (+); (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 (+).  
 285



286  
 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 autochthonous tree species. (ii) Forest vascular plant  
340 species richness gained 77% above four autochthonous 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 autochthonous 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 autochthonous 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

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 (Löhmus et al. 2007)  
400 less crucial than logs for this taxon (Humphrey et al. 2002). Finally, Tönnerberg (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 ectomycorrhizic 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 autochthonous 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 autochthonous 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

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