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

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Abstract

To encourage forest managers to use biodiversity indicators in their work, providing environmental variables that depict species habitats, have well-calibrated and strong relationships with biodiversity and are easy to routinely record would be a step forward. The Index of Biodiversity Potential (IBP) is a rapid habitat assessment method widely used in France. It uses ten variables that indicate potential habitat for forest-dwelling species and is easy for forest managers to implement during their day-to-day activities. The objective of this paper is to evaluate the indicator power of these IBP variables at the stand scale, i.e. their capacity to co-vary with empirical species richness and composition data for nine taxa. The data were obtained from 487 plots set up in 19 forested areas in France. Taxonomic data focused on corticolous lichens, corticolous and saproxylic bryophytes, polypores, saproxylic beetles, ground beetles, hoverflies, birds, bats and vascular plants. For the latter five taxa, we built subgroups of forest-specialist species. The IBP variables were recorded on 1-ha circular plots centered on the sampling point used to record taxonomic data. We explored the relationships between the IBP variables and species composition/richness of nine taxa at the stand scale. Furthermore, we searched for threshold values for all the significant relationships found between species richness and the IBP variables. Variations in the species composition of vascular plants and saproxylic beetles, and to a lesser extent, polypores, bats and lichens, were significantly related to habitat variations (ranked according to the Procrustes significance level). The contribution of the IBP variables to the total inertia of species composition was about 18.7% on average. The IBP variables had a lower number of significant relationships with species richness than with species composition. Unexpectedly, the forest subgroups mainly showed fewer significant relationships with habitat variables than did the full-groups, both for species richness and composition. We highlighted seven significant thresholds in the habitat variables above which species richness was significantly higher. Finally, we recommend that forest managers (i) routinely use a rapid habitat assessment such as the IBP, (ii) orient silvicultural practices to ensure conservation of autochtonous tree species, large logs and different types of aquatic habitats above the thresholds highlighted in this study, and (iii) periodically complete a biodiversity assessment at the forest scale by recording taxonomic data.

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

Highlights

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

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.

We chose to focus on species subgroups such as forest specialists (Gosselin 2012), since they are often the main targets of forest conservation, and to emphasize the stand scale, since it is the main operational scale for forest managers (Failing and Gregory 2003). The habitat variables the most commonly tested at the stand scale in previous studies have been tree age, tree canopy cover, deadwood volume and deadwood diversity (Gao et al. 2015). Few studies have tested other variables such as shrub cover, vertical stratification, stand basal area, tree height, volume of standing trees, TreMs or tree species composition (Gao et al. 2014; Gao et al. 2015). However, most of these variables require not only field measurements but also subsequent calculations. The objective of our study was to evaluate habitat variables that are easy to record in the field without specialized devices and that do not require post-calculations for their indicator power at the stand scale. We therefore used the ten variables already selected for a rapid habitat assessment method designed for routine use in the field: the Index of Biodiversity Potential (IBP; Larrieu and Gonin 2008). The IBP index is already being used in France by many forest managers. It combines ten factors deemed to favor biodiversity, most of which focus on precise items either already typically observed by managers for economic issues, or easy to observe in the field without any tools or devices. We investigated the relationships between empirical species richness and composition data for nine taxa according to these ten variables.

2. Material and methods

Taxonomic data were recorded following standardized procedures at the stand level, within the framework of several different research projects (Table A1 in Supplementary Material). We used data from 487 plots situated in 19 French forested areas (Fig 1). The wide range of forest contexts sampled represented both the Atlantic and Continental zones, forests from lowlands to highlands, and broadleaved, conifer-dominated and mixed stands (Fig. 1 and Table A2 in Supp. Mat.)

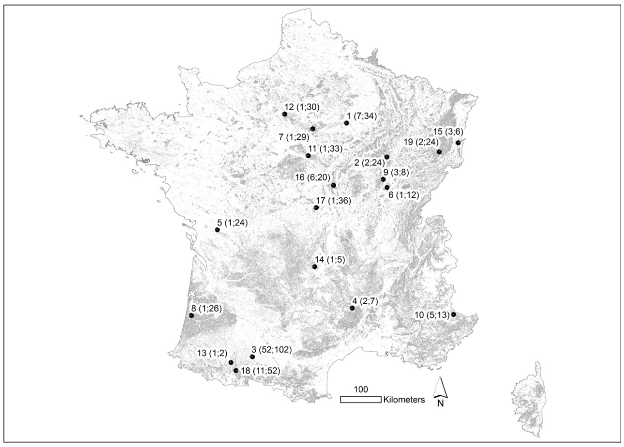

Fig. 1. Map of the 19 forested areas sampled; in brackets for each area, the number of forests sampled followed by the number of sampling plots; 1:Aube, 2:Auberive, 3:Coteaux de Gascogne, 4:Cévennes, 5:Chizé, 6:Citeaux, 7:Fontainebleau, 8:Landes de Gascogne, 9:Lavaux, 10:Mercantour, 11:Orléans, 12:Rambouillet, 13:Rebisclou, 14:Rhue, 15:Taillis.A, 16:Taillis.B, 17:Tronçais, 18:Vieilles Forêts des Pyrénées, 19:Vosges

2.1. Rapid forest habitat assessment

All the stands were characterized by the same observer on a 1-ha circular plot centered on the sampling point where taxonomic data were recorded. The observers followed the protocol for the Index of Biodiversity Potential (IBP; Larrieu and Gonin, 2008), which includes attentive observation while crisscrossing the stand. Nine of the ten IBP factors belong to three broad categories: (i) living vegetation: number of native tree-species and number of vertical strata; (ii) deadwood and TreMs: number of large snags, large lying deadwood items, very large trees and living TreM-bearing trees; (iii) associated features: open areas, number of aquatic macrohabitat types and rocky macrohabitat types. In addition, we replaced the broad IBP variable "*Number of TreM-bearing trees*" by its seven constituting variables *(Table 1);* these variables were used only for relationships between habitat variables and species richness. In all then, a total of 16 compositional and structural stand characteristics (Table 1) were simultaneously recorded on site.

Ancientness is also taken into account by the IBP protocol as an additional factor since recent and ancient forests show significant differences in biodiversity (Assman 1999; Gossner et al. 2008; Hermy et al. 1999; Diedhiou et al. 2009). In France, a military survey map showing land use over a large part of the territory (called "Etat Major") was published in the mid-19th century.; Current forests already indicated on this map are considered likely to have never been cleared or replaced with another land use (Dupouey et al. 2002). Ancientness was post-recorded at the office.

Finally, we recorded four other covariables: biogeographic domain, location of forested area, altitude and dominant tree-species (Table 1). Hereafter, the term "habitat variables" refers to the IBP constituting variables, while "environmental variables" refers to the total pool of both IBP constituting variables and the four covariables mentioned above.

Since the aim of this study was to assess the potential of routine variables as robust habitat surrogates for certain taxa, and not to assess the relevance of the IBP index per se, we did not test the IBP scoring system.

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

				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)*	-	-	-

2.2. Taxonomic data

Our study targets nine taxa that are widespread in forest ecosystems covering, *a priori*, a wide range of habitat requirements. Four taxa were intrinsically associated with forests, trees, woody substrates or forest-buffered climatic conditions: corticolous lichens, corticolous or saproxylic bryophytes, polypores and saproxylic beetles. Five other taxa– namely ground beetles, hoverflies, birds, bats and vascular plants - had a more heterogeneous ecology. Based on Coulon et al. (2000), Speight et al. (2015), Cramp et al. (1980-94) Arthur and Lemaire (2009) and Rameau et al. (1989, 1999), respectively, we singled out forest specialist subgroups in the assemblages of these five taxa. We defined the subgroups as follows: (i) the forest ground beetle subgroup includes species that are mainly observed in forest ecosystems; (ii) the forest bird subgroup includes species that are mainly observed in forest ecosystems, including tree cavity-dwellers; (iii) the forest bat subgroup includes species using cavities or peeling-barks for resting or breeding; (iv) the forest vascular plant subgroup includes species that are able to grow under closed canopy. Ultimately, we gathered data on one to seven taxa per plot (Table A3) for a total of 14 taxonomic variables (i.e. 9 full groups plus 5 subgroups). (Table A4). Sampling procedures are specified in Table A1.

2.3. Data analyses

All the analyses were performed at the plot level. Since several taxa were recorded for presence/absence only (e.g. polypore, bats, bryophytes, lichens), we did not use abundance values in the analyses.

2.3.1. Compositional analysis

First, we explored the congruence between the between-plot dissimilarity matrix based on pooled habitat variables (see the set of metrics in Table 1) and the between-plot dissimilarity matrix based on species composition (for each of the nine taxa). To do so, we performed a Procrustes rotation on non-metric multi-dimensional scaling (NMDS) ordinations (Peres-Neto and Jackson 2001) of the Bray-Curtis dissimilarity matrix for habitat variables and the Jaccard dissimilarity matrix for species occurrence data. Permutation tests associated to the Procrustes method (*protest* function, R-package *Vegan*, with the m^2 Procrustes statistic; number of runs=1,000) revealed the non-randomness of the congruence in fit between multivariate data tables. In order to account for the nested structure of our dataset, permutations were conditioned upon forested area, which was a stratifying variable. Next, we performed a Canonical Analysis of Principal Coordinates (CAP, Anderson and Willis 2003; *capscale* function, R-package *Vegan*) to investigate the effects of each habitat feature on variations in species composition for each taxonomic assemblage. Inertia was partitioned from Jaccard's distance matrices (*vegdist* function, R-package *Vegan*) on all explanatory habitat variables, since co-linearity among predictor variables is not a problem in CAP (Anderson and Willis 2003). After partialling out the geographical effect (i.e. forested area), both in the full CAP combining all the habitat variables and in the individual CAPs performed for each habitat variable, we calculated the proportion of inertia cumulatively explained by all the habitat variables, the relative total contribution (intrinsic + co-explained) of each habitat variable to the total inertia and the statistical significance of this contribution (by means of permutation tests - 999 runs).

2.3.2. Species richness analysis

We used multi-model averaged estimates (Burnham and Anderson 2002) to determine the relationship between each of the 14 taxonomic variables for species richness and each of the environmental variables. For each response variable (count data), we generated Poisson Generalized Linear Mixed Models (GLMM, *glmer* function, R-package *lme4*). The mixed models enabled us to include forested area as a random variable. Since co-linearity among predictor variables may lead to unreliable parameter estimates, we followed the strategy suggested by Zuur et al. (2010) to address the multicolinearity problem before model averaging. First, we sequentially dropped the covariate with the highest variance inflation factor (VIF; *vif.mer* function from Frank 2011), then recalculated the VIF; we repeated this process until all VIFs were below the cutoff value of 3 suggested by Zuur et al. (2010). Then, we generated models with all the combinations of the remaining variables and calculated the differences in the Akaike information criterion (AICc, Burnham and Anderson 2002) scores between each model and the null model (dredge function, R-package MuMIn). We also calculated the Akaike weights for each model (model.avg function, R-package MuMIn). Finally, we selected the best two-variable models. Since our aim was to highlight habitat variables as bio-indicators and not to explain taxonomic communities, we did not account for a priori ecological links between the taxon and the habitat variables.

Furthermore, we checked the significant relationships (at $p<0.01$) between habitat variables and species richness in the GLMM for thresholds. Threshold values were calculated by recursive partitioning and derived from estimates of breakpoints by means of maximally selected two-sample statistics (Hothorn and Hornik 2006; *ctree* function, R-package *party*). This method provides a conditional inference tree with p-values for one or more critical thresholds. When using the *ctree* function, the model is constrained and does not allow any co-variables or random effects to be taken into account. To deal with this issue, we kept only the most significant results: only primary nodes with highly significant ($p < 0.001$) thresholds were selected, and only if the number of plots was greater than 30 on either side of the threshold. Then, 95% confidence intervals (bootstrap percentile interval) were calculated for all the selected thresholds, based on 1,000 bootstrap samples (*boot.ci* function, R-package *boot*).

In order to standardize sampling effort and to account for missing data for saproxylic beetles, ground beetles and hoverflies (traps destroyed by animals, wind, rain or humans), we used the log of a corrected factor based on the number of undisturbed sampling months as an offset in our models. For vascular plants, we considered the data to be comparable whatever the area sampled (ranging from 600 to 1018 m^2) since (i) the observers took care to maintain homogeneous local conditions (phytosociological-type sampling), (ii) in forest types similar to those we sampled, Archaux et al. (2007) highlighted samplings set up on areas above 400 m^2 are comparable, and (iii) the sampled surface area was constant in each forested area (used as a grouping variable in the models). Fungi were sampled along a gradient of one to three years, with one to three runs per year; we therefore only retained polypore records in our analysis, since their sporophores are long-lasting. Bird data was recorded inside 25, 100, and outside 100 m-radius areas; since environmental variables were recorded on 56 m-radius plots (i.e. 1-ha plots), only bird data recorded inside a 25 m-radius area were retained (see Table A1 for details).

3. Results

3.1. Variations in species composition

Habitat variations significantly ($p<0.01$) reflected variations in species composition for vascular plants and saproxylic beetles, and to a lesser level of significance ($p<0.05$) for polypores, bats and lichens. However, they did not reflect variations in species composition for ground beetles, birds, bryophytes or hoverflies (Table 2).

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

3.2. Habitat variables as indicators of biodiversity

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

Individual habitat variables did not contribute very much (from 0.46 to 58.03%) to variations in species composition (total inertia) as estimated by CAP (Table A4). However, when we tested the whole set of nine recorded variables (or 10 if ancientness could be determined), excluding the “forested area” random effect, contributions ranged from 6.05% (for saproxylic beetles) to 88.33% of the total inertia (for lichens) (Table A4, last column).

We found numerous significant relationships between habitat variables and species composition (Fig. 2; details in Table A4). Vascular plants, saproxylic beetles and polypores showed the largest proportion of significant relationships tested (100%, 100% and 80%, respectively, at $p<0.05$). On the other hand, we did not find any significant relationships between habitat variables and bats (Table A4). However, the set of habitat variables contributed to 9.5% of bat inertia.

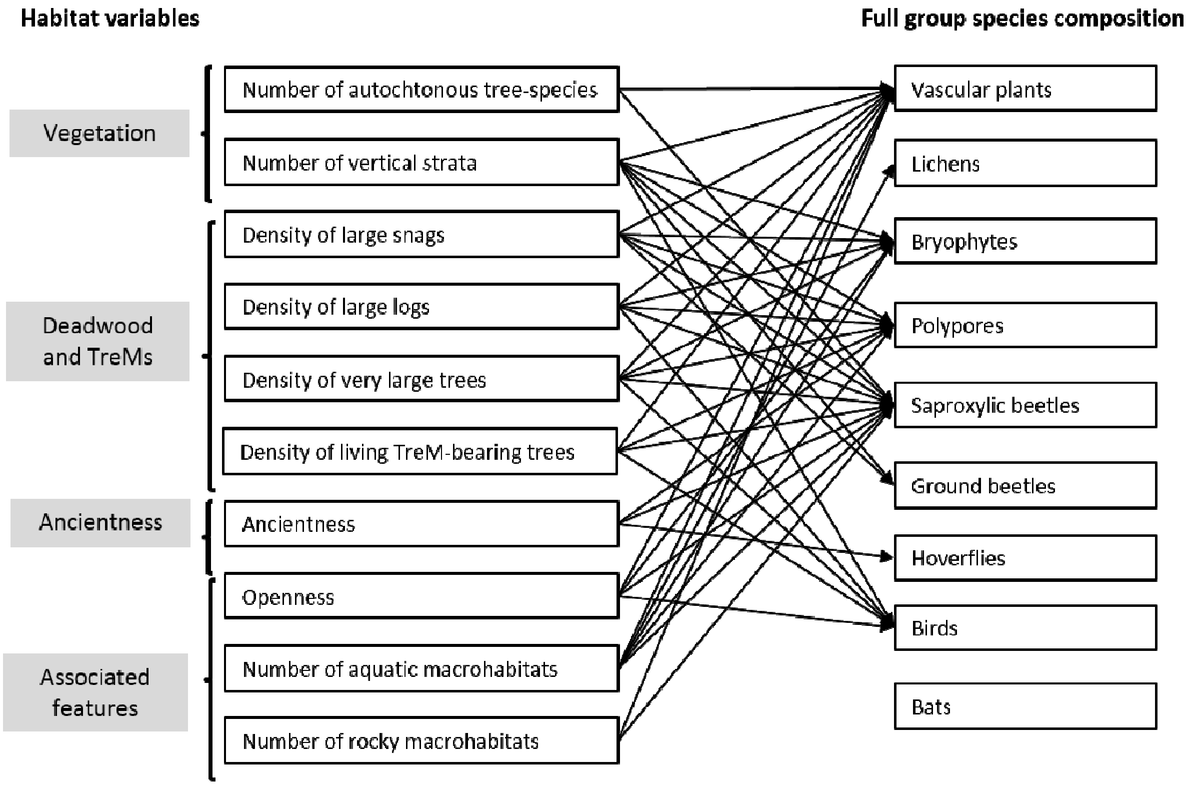

Figure 2. Relationships between the ten habitat variables (left) and inter-plot variation in species composition (right) for nine taxa (full groups) at the plot scale; only significant relationships at $p<0.01$ are shown (solid arrows); TreMs: tree-related microhabitats; ancientness was tested for only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

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 (+);

(iv) the density of trees with crown deadwood on hoverflies (-); (v) the density of polypore-bearing trees on polypores (+); (vi) the density of trees with missing bark on both polypores(+) and hoverflies (+); (vii) the density of cracks on saproxylic beetles (+); (viii) openness on both vascular plants (+) and saproxylic beetles (+); (ix) the number of aquatic macrohabitats on vascular plants (+), polypores (+) and saproxylic beetles (+); and (x) the number of rocky macrohabitats on saproxylic beetles (+).

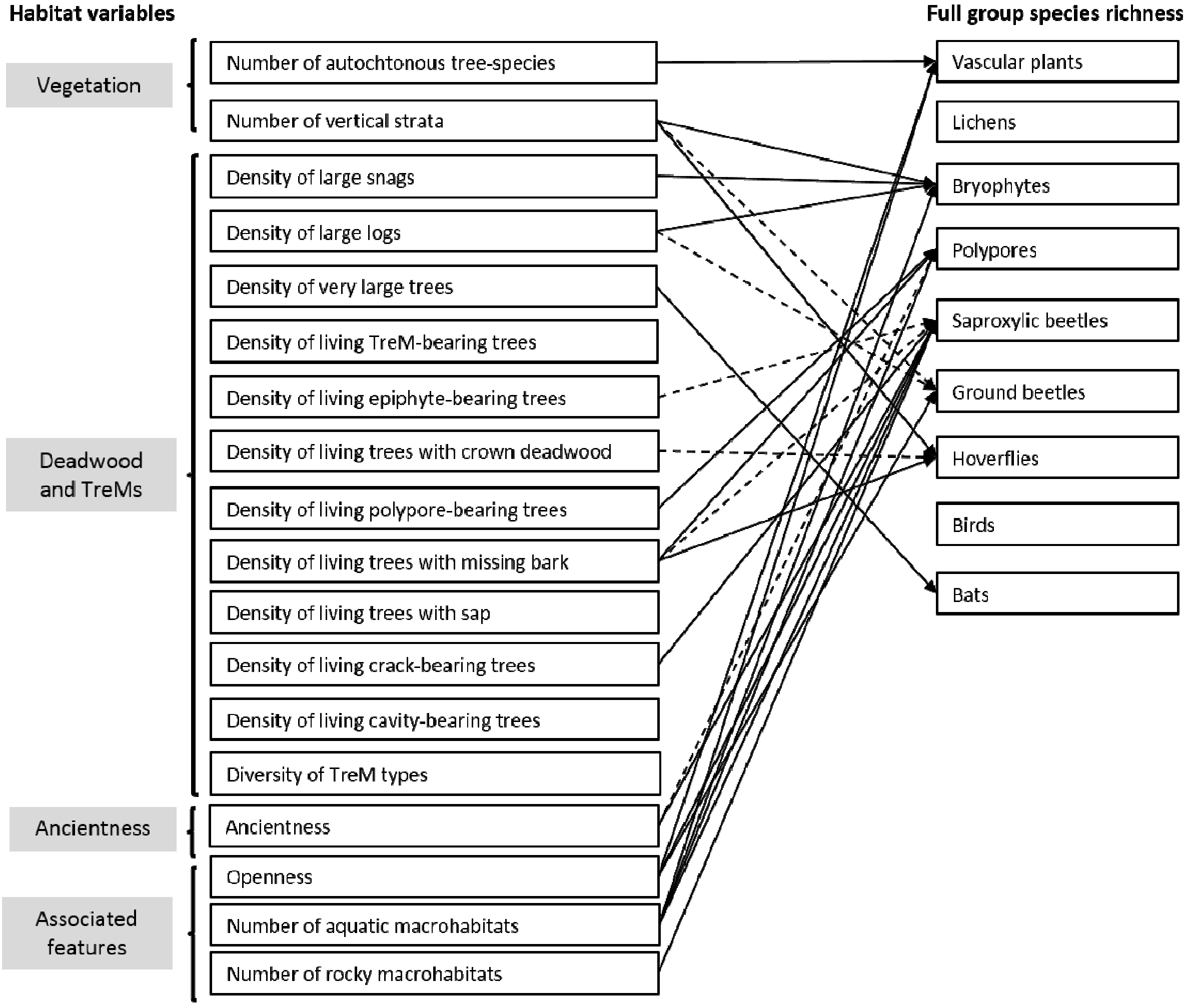

Figure 3. Relationships at the plot scale between 18 habitat variables and the species richness of 9 taxa (full groups); significant relationships at p<0.01 are shown by solid or dashed arrows for positive and negative relationships, respectively; TreMs: tree-related microhabitats; ancientness was tested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

Furthermore, the species richness of saproxylic beetles at the plot scale was positively affected by increasing altitude, non-Atlantic geographical location and dominance of broadleaves (Table A5).

Increasing altitude also had a positive effect on the species richness of bryophytes while it had a negative effect on that of vascular plants.

The two most common habitat variables in the best two-variable models for species richness were number of tree-species (n=5) and number of aquatic macrohabitats (n=5) (Table 3). The best model for saproxylic beetle diversity included only covariables.

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

Briefly, the habitat variables with the highest number of significant (p<0.05) effects on taxa (full groups) were: (i) **for species composition**, the density of large snags (n=8), the density of large logs (n=6), the density of very large trees (n=6), the number of vertical strata (n=6), the number of aquatic macrohabitats (n=6), the density of TreM-bearing trees (n=5), and openness (n=5); and (ii) **for species richness**, the number of vertical strata (n=5), the number of aquatic macrohabitats (n=5) and the density of large logs (n=4).

Except for lichens, hoverflies, birds and bats, we found at least one significant (p<0.01) habitat driver for every taxon, **both for species richness and composition** (Fig. A1; details in Tables A4 and A5). Among these significant habitat drivers, only five affected two or more taxa: (i) the number of vertical strata for bryophytes and ground beetles, (ii) the number of large snags for bryophytes and saproxylic beetles, (iii) ancientness for polypores and saproxylic beetles, (iv) openness for vascular plants and saproxylic beetles, and (v) the number of aquatic macrohabitat types for vascular plants, bryophytes, polypores and saproxylic beetles.

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

Unexpectedly, most of the forest subgroups showed fewer significant relationships with habitat variables than did the full-groups. This was true for both species richness and composition (Fig. A2 for species composition, Fig. A3 and Table A5 for species richness). Only forest vascular plant species composition showed a number of significant relationships similar to the corresponding full group. Furthermore, as with the full taxonomic groups, none of the habitat variables significantly affected all the forest groups combined, either in terms of species richness or species composition. The density of large logs and openness had a significant effect on the species composition of three out of the four forest groups (namely forest vascular plants, forest birds and forest ground beetles). Only forest birds showed the same best 2-term models for species richness as the related full group (Table 3). We did not reveal any clear driver for forest bats for either species richness or species composition.

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

We found seven significant ($p<0.001$) threshold values at the 1ha-plot scale for the following positive (+) or negative (-) significant ($p<0.01$) relationships between habitat variables and the species richness of the 14 studied taxonomic groups (Table 4 and Fig. A4, A5, A6, A7, A8 and A9). (i) Vascular plants gained 50% in species richness above four autochtonous tree species. (ii) Forest vascular plant species richness gained 77% above four autochtonous tree species. (iii) Bryophyte species richness gained 15% above three large logs. (iv) Polypore species richness gained 340% above one aquatic macrohabitat. (v) Forest ground beetle species richness gained 40% above one polypore-bearing tree. (vi) Forest ground beetle species richness gained 75% above one tree with missing bark. Finally, (vii) Ground beetle species richness lost 69% above three strata.

Table 4. Significant thresholds ($p<0.001$) in positive relationships between habitat variables and taxon species richness at the 1ha-plot scale (see Table A5); Magnitude: relative increase/decrease between median values below and above the threshold; CI 95: confidence interval at 95% (5,000 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

4. Discussion

Among the numerous results relating the species composition and diversity of the studied taxonomic groups to the selected environmental variables, most were expected. However, a few were surprising in ecological terms. For example, we found positive relationships between saproxylic beetle species richness and the number of aquatic and rocky macrohabitats. However, aquatic and rocky macrohabitats often result in a higher degree of stand openness when they occur, and we show that openness favors higher saproxylic beetle species richness. The negative relationship between hoverfly species richness and the density of trees with crown deadwood was equally surprising since several hoverfly species do use crown deadwood during their larval stage (Speight et al. 2015). These results may be due to the systematic selection of the explanatory variables we applied to our models, which we did not base on ecological hypotheses; or by indirect effects related to more efficient sampling of hoverflies with our flight interception traps in open stands than under a dense canopy. Higher hoverfly species richness has been observed in open stands (Gittings et al. 2006). Indeed, more open stands provide the species-rich herb layer adult hoverflies need as a source of pollen and nectar (Fayt et al. 2006), although several forest species are saproxylic at the larval stage and often depend on various saproxylic substrates in mature closed-canopy stands (see also Herrault et al. 2016).

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

Most of the previous studies dealing with the relationships between habitat variables and taxa have focused on species richness alone (Gao et al. 2015). However, we found more significant relationships between habitat variables and species composition than between habitat variables and species richness. Only 16% of the tested relationships were significant (at $p<0.01$) for both species richness and composition. This confirms that species composition is relevant when selecting biodiversity surrogates and investigating the relationships between biodiversity and habitat variables. Indeed, species composition provides results complementary to those obtained through a species-richness approach for cross-taxon congruence (Larrieu et al. 2018; Jokela et al. 2018). However, species composition is slightly more difficult to interpret than species richness, especially in terms of the magnitude of the relationship. Alternative approaches, not pursued here, include using more precise ecological subgroups (Barbier et al. 2009; Gosselin 2012; Zilliox and Gosselin 2014) or performing analyses at the species level (Okland et al. 1996; Bouget et al. 2014b). However, the practical comprehensive life-trait databases required by such approaches are available for very few taxa (e.g. Syrph the Net for hoverflies; Speight et al. 2015) and most life-trait descriptions must therefore be collected from a variety of dispersed sources.

4.2. New insights on relationships between habitat variables and biodiversity

Most of the relationships we found between the habitat variables and species richness were positive (77%). However, the number of vertical strata, the density of large logs, the density of trees with missing bark and ancientness showed both positive and negative relationships, depending on the taxon.

We found that the density of large logs was a relevant variable for the species richness of corticolous and saproxylic bryophytes, which is partly in line with Söderström (1988a, b), Andersson and

Hytteborn (1991) and Sabovljevic et al. (2010) who revealed a positive relationship between log diameter and the frequency of saproxylic bryophytes. We also revealed that the density of large snags was a relevant indicator for the species richness of corticolous and saproxylic bryophytes, although snags had previously been highlighted as a bryophyte-poor substratum (Lõhmus et al. 2007) less crucial than logs for this taxon (Humphrey et al. 2002). Finally, Tönnberg (2001) found no correlation between the local amount of deadwood and the species richness of saproxylic bryophytes. We therefore conclude that focusing on any large deadwood items (both logs and snags) may be a simpler yet efficient way to check for bryophyte diversity with a view to conservation. Ancientness is known to influence assemblage composition for true bugs (Gossner et al. 2008), ectomycorhizic fungi (Diedhiou et al. 2009), soil fauna (Janssen et al. 2018) and - among the taxa in this study - vascular plants (e.g. Hermy and Verheyen 2007; Dupouey et al. 2002), ground beetles (Assmann 1999), saproxylic beetles (Brin et al. 2016; Janssen et al. 2016, 2017), hoverflies (Herrault et al. 2015), bryophytes and epiphytic lichens (Rose 1993; Fritz et al. 2008; Janssen et al. 2019). Unfortunately, we were not able to test for an ancientness effect on the species composition of bryophytes, lichens, bats, birds and vascular plants since our sampling design was very unbalanced. However, like Herrault et al. (2015), we found that ancientness was a key feature for species composition in hoverflies for the full group (but not for forest-specialists alone). Contrary to Assmann (1999), we did not find that ancientness influenced ground beetle assemblages. Finally, we found that ancientness is relevant for the species richness of polypores, though unexpectedly, the relationship was negative. To our knowledge, this is an original result. However, it should be noted that our sampling design had a high proportion of young stands hosting pioneer tree species, which can quickly provide saproxylic substrates due to their short lifespan, thus promoting high polypore diversity. Although we found lower polypore species richness in ancient forests, the highly significant relationship between ancientness and the composition of polypore assemblages showed that this factor does play a role in fungus conservation by promoting specific species.

The variable “number of autochthonous tree-species” occurred in 36% of our best models for species richness. This relationship was expected for vascular plants since i) species richness for non-woody plants, shrubs and trees are all positively influenced by the nutrient richness of the soil (e.g. Rameau et al. 1999) and ii) both tree seedlings and small saplings are commonly included in the vascular plant sample. A similar relationship was also expected for forest hoverflies, bats and birds since a stand encompassing a mix of tree species provides a wider range of both feeding resources for hoverfly larvae and resting and breeding microsites for bats and birds than does a pure stand. Mixed stands better match the requirements of different taxa (e.g. Cramp et al. 1980; Arthur and Lemaire 2009; Speight et al. 2015).

The variable “number of aquatic macrohabitats” occurred in 36% of our best models for species richness and was relevant for the species composition of six out of nine taxa (full groups). This type of habitat is often considered specific to aquatic taxa only, whereas our findings suggest that aquatic macrohabitats could be more widely used as an indirect indicator of wet conditions in general.

4.3. Most of the forest taxonomic subgroups showed weaker relationships with habitat variables than did full-groups

We built forest subgroups for bats, birds, hoverflies, ground beetles and vascular plants since (i) forest-specialist species are often targeted for conservation by forest managers who use an integrated approach, and (ii) we expected stronger relationships than for the full groups since the latter encompass species ranging beyond forest conditions. However, we found more numerous significant relationships between full groups and habitat variables than we did for forest subgroups alone. Several reasons may explain this result. First, the life-trait databases or the variables we used to build our forest subgroups may not have been completely relevant. For example, dwelling in cavities or under peeling bark may not be the most relevant feature for forest-specialist bats, very few of which are strict tree-roosters; most also make use of similar microhabitats provided, for instance, by buildings (Arthur and Lemaire 2009). Secondly, forest specialists may mainly depend on habitat variables we either did not record or recorded too broadly (i.e. our variables may not have focused on features specific enough to definitely select the forest specialist), or which we did not record at the most appropriate spatial scale. Thirdly, taxa such as hoverflies are multi-habitat users, i.e. saproxylic species need deadwood substrates while all adults need flower resources (Speight et al. 2015). This means that the presence of saproxylic hoverflies is mostly linked to the co-occurrence of both deadwood and flowering plants in the same stand. Another explanation might be that only a part of the habitat feature is included in the IBP variables; for example, only deadwood items over 40 cm in diameter are recorded and, although these large items are crucial for biodiversity (e.g. Gossner et al. 2013), most saproxylic species require a wider range of diameters. Finally, the relationship with the non-forest species in the full group may have actually been stronger than with the forest specialists.

Stronger relationships between habitat variables and non-forest vascular plants than with forest vascular plants have already been found (Barbier et al. 2009; mostly Zilliox and Gosselin 2014).

Among bryophytes, forest-specialists do seem to have stronger relationships with forest habitat variables than do the other species in the taxon (Gosselin et al. 2014). Yet a practical life-trait database relevant for France is lacking since the databases available in Europe to date are limited to the UK (Hill 2007) and Germany (Schmidt 2013).

4.4 From ecological results to forest management guidelines: providing thresholds

When we analyzed our species richness models in terms of the magnitude of the relationships (as in e.g. Barbier et al. 2009 and Zilliox & Gosselin 2014), we found rather strong relationships between habitat variables and species composition, and weak (though sometimes significant) relationships between habitat variables and species richness, with one notable exception (the relationship between the number of strata and hoverfly species richness). Yet, threshold analyses revealed some strong, non-linear relationships between certain habitat variables and species richness for some taxa. Forest management encompasses a wide range of technical, economic and environmental aspects, and covers a wide array of disciplines. Therefore, managers are often faced with complex trade-offs. Simple and efficient guidelines can help them better integrate biodiversity issues in both management plans and technical procedures. Critical thresholds for taxon response to habitat variations are among the simplest tools (Müller and Bütler 2010). Significant thresholds at the stand scale for crucial deadwood amounts (Müller and Bütler 2010; Gossner et al. 2013), optimum range of canopy openness, proportion of deciduous trees and optimum stand age (Moning and Müller 2008, 2009) have already been published for snails, birds, saproxylic beetles, fungi, mosses and lichens. In our case, we did not record stand age since most of the stands we sampled were uneven-aged. For deadwood, we used a complementary approach. First, we chose density rather than total volume for deadwood items since assessing density does not require measurements or calculations and is easier for occasional forest managers (e.g. owners of small woodlands) to use. Second, we focused on particular features such as large deadwood items or very large trees, which are typically rare in managed forests (Bauhus et al. 2009, Paillet et al. 2015) yet are relevant for saproxylic beetles (Gossner et al. 2013), fungi or forest bryophytes (Gosselin et al. 2014, 2017), among others. We provide seven significant thresholds. Among them, five thresholds seem to be related to ecological requirements: the number of autochtonous tree species for vascular plants (both full- and forest subgroup; positive relationship; see discussion above), the density of large logs for bryophytes (as crucial substrates; positive relationship), the number of aquatic macrohabitats for polypores (positive relationship; probably because wet conditions favor the growth of fungi), and the number of vegetation strata for ground beetles (negative relationship; ground beetles are mostly heliophilous and mainly associated to non-forest ecosystems). The two others, i.e. the density of living polypore-bearing trees and trees with missing bark for forest ground beetles, are likely to hide correlations with other ecological factors, and this may reduce their relevance in contexts outside the range of forest types we studied.

Gosselin et al. (2014) showed that using other statistical methods (taking into account random effects, specific probability distribution, spatial autocorrelation and other continuous sigmoid functions) led to larger confidence intervals around thresholds. Furthermore, an ongoing study highlights that variations in threshold values among forest sites (and also the curve pattern) may have an impact on estimations of the magnitude of the relationships (Godeau et al. submitted). As in Gosselin et al. (2014) and Godeau et al. (submitted), the inclusion of non-linear relationships allowed us to detect strong relationships with species richness, while the use of (generalized) linear models only mostly revealed only weak relationships. Further research should therefore focus on properly estimating thresholds and non-linear relationships between habitat variables and biodiversity metrics for a large range of taxa and forest contexts. However, since we used highly demanding criteria and kept only the most significant thresholds, we are confident that our thresholds are relevant for the conservation of the concerned taxa in temperate forests.

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

The Procrustes approach showed that the ten IBP habitat variables considered together were relevant when assessing variations in species composition for five of the nine taxa studied (56%). Further research should consider variations in functional diversity and use taxon life-traits in order to evaluate whether the variations in species composition are related to functional changes. It would also be relevant to test covariations on key taxa for ecosystem functioning such as soil-dwellers (e.g. Zanella et al 2017). Managers would respond more readily to demands for biodiversity preservation if the changes they implement resulted in better ecosystem functioning.

This study highlights numerous significant relationships between individual habitat variables and biodiversity and provides practical thresholds for management. However, none of the habitat variable combinations consistently explained the variations in species richness for all the taxa studied. Furthermore, the contribution of the habitat variables to total species composition inertia was relatively low (median=10.4%, mean=15.9, range: 6-88%). The limited explanatory power of our environmental indicators for biodiversity can be linked to several effects. First, nonlinear effects may be at play (Araujo et al. 2003); this is consistent with our findings that threshold non-linear models gave stronger relationships than did generalized linear models for species richness. Second, the suitable niches might not have been fully occupied due to time-lag responses (Cristofoli and Mahy 2010; Jackson and Sax 2010). In addition, non-environmental factors may have been predominant biodiversity drivers (Hortal et al. 2009). Finally, our taxonomic samplings could have been incomplete, or other environmental factors not considered in our study could have been involved.

6. Conclusion and research perspectives

It is relevant in a funds-limited context to consider an indicator in terms of both performance and cost. Environmental indicators are easy to assess during routine management activities and are the cheapest indicators for species richness in Mediterranean ecosystems (Mandelik et al. 2010). Furthermore, recording taxonomic data is time-consuming and costly, even though it is possible to pre-select taxa by optimizing the cost/performance ratio (Gardner et al. 2008; Larrieu et al. 2018). Schamberger (1988) and Noss (1990) believe that monitoring both habitat and taxa is essential in most cases. Landres et al. (1988) also recommend mixing taxonomic and environmental indicators while Ferris and Humphrey (1999) suggest using a combination of several structural and compositional indicators. Composite data sets combining both taxonomic and environmental data have already demonstrated their efficiency and have led to progress in biodiversity protection (Pressey 2004; Cowling et al. 2004). To go further, Vierikko et al. (2010) suggest using a combination of taxonomic, environmental and socio-economic indicators to monitor sustainable forestry goals. According to Duelli and Obrist (2003), an index combining a set of indicators is the best approach. Based on the combined results of this study and those of a companion study assessing cross-taxon congruence patterns and the cost-efficiency of surrogate taxa (Larrieu et al. 2018), we propose the following recommendations to help forest managers promote more biodiversity-friendly forest management: (i) routinely apply a rapid habitat assessment such as the IBP; (ii) use appropriate silvicultural techniques to increase or maintain autochtonous tree diversity and the density of large logs above the thresholds highlighted in this study; (iii) conserve the diversity of aquatic habitats; and (iv) periodically carry out a biodiversity assessment at the forest scale by recording taxonomic data focusing on saproxylic beetles and vascular plants, or on saproxylic beetles, vascular plants and birds (the most cost-efficient associations, according to Larrieu et al. 2018).

Due to the wide range of taxa and forest types sampled in this study, we believe our findings and recommendations are relevant at the stand scale for temperate European forests. However, further research would be welcome since (i) most of our taxonomic data are related to a single sampling year; ii) habitat variables were only recorded at the stand scale (landscape-level environmental variables should also be recorded); (iii) only one metric was used to evaluate alpha diversity (i.e. species richness); (iv) we used presence/absence data to be consistent among the taxa but adding abundance data could be beneficial; and (v) statistical analyses could be improved (e.g. non-linear approaches, consideration of more random effects). Research should also consider broader temporal (Favreau et al. 2006) and spatial scales (Yoccoz et al. 2001, Bouvier et al. 2017) as well as take into account adjacent habitats and their management, in particular for small woodlands (Tölgyesi et al. 2018). Research should also consider some poorly-known and very diverse taxa, which play a key role in ecosystem functioning, such as soil fauna, Diptera other than hoverflies, moths, fungi other than polypores and parasitoid Hymenoptera.

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