

## Original articles

## Cost-efficiency of cross-taxon surrogates in temperate forests

Laurent Larrieu<sup>a,b,\*</sup>, Frédéric Gosselin<sup>c</sup>, Frédéric Archaux<sup>c</sup>, Richard Chevalier<sup>c</sup>, Gilles Corriol<sup>d</sup>,  
Emmanuelle Dauffy-Richard<sup>c,1</sup>, Marc Deconchat<sup>a</sup>, Marion Gosselin<sup>c</sup>, Sylvie Ladet<sup>a</sup>,  
Jean-Marie Savoie<sup>a</sup>, Laurent Tillon<sup>e</sup>, Christophe Bouget<sup>c</sup>

<sup>a</sup> UMR 1201 DYNAFOR, INRA, INPT, INPT-EI Purpan, Université de Toulouse, 31320, Auzeville Tolosane, France

<sup>b</sup> CRPF-Occitanie, antenne de Tarbes, Place Du Foirail, 65000, Tarbes, France

<sup>c</sup> Irstea, UR EFNO, Domaine des Barres, 45290, Nogent-sur-Vernisson, France

<sup>d</sup> CBNPMP, Vallon Du Salut, 65000, Bagnères de Bigorre, France

<sup>e</sup> ONF DFRN, 2, Avenue De Saint-Mandé, 75570, Paris Cedex 12, France



## ARTICLE INFO

## Keywords:

Biodiversity assessment  
Cross-taxon congruence  
Species richness  
Species composition

## ABSTRACT

Cross-taxon surrogacy (between-taxon similarities in species patterns) can help conservation biologists to design simplified, standardized and efficient tools for biodiversity monitoring. Our study aims to identify potential sets of indicator taxa to be recommended in temperate forests. We focused on nine forest taxa: vascular plants, bryophytes, saproxylic beetles, polypores, lichens, ground beetles, hoverflies, birds and bats. We assessed cross-taxon congruence patterns, in terms of both alpha and beta-diversity, using empirical biodiversity data from 206 plots in ten French forested areas. We evaluated the cost-efficiency of potential surrogate taxa using both strictly encoded expert knowledge and results of this study. The most congruent taxa in alpha-diversity were bryophytes (with bats and polypores), and ground beetles (with bats and saproxylic beetles), though levels of covariation were mostly weak. The most congruent taxon in beta-diversity was vascular plants (with bryophytes, ground beetles, lichens and forest birds). Contrary to our expectations, the subsets of forest species within a given taxon exhibited a lower surrogacy than the taxon as a whole. Four categories of taxa were delineated based on cost-efficiency scores – from costless but ineffective (bats and ground beetles) to costly but effective (saproxylic beetles and polypores). No single taxon was firmly identified as a relevant surrogate for other taxa; using a set of two or three taxa drastically increased surrogacy, compared with single-taxon approaches. Saproxylic beetles associated with vascular plants, or with both vascular plants and birds, seemed to be the most cost-efficient associations. Further research is required to up-scale our results from the short-term, local scale to the long-term, landscape scale in European temperate forests.

## 1. Introduction

Since the Helsinki conference in 1993, when the concept of sustainable management in forest ecosystems became mandatory, managers have been required to maintain species diversity in managed areas (FAO, 1999). However, assessing forest biodiversity is challenging due to (i) the large number of species involved, which discourages full inventories, (ii) the wide variety of species behavior and habitat requirements, which requires sampling according to multiple methods and procedures, and (iii) the difficulty of species identification for many taxa. Therefore, to reach their goals, forest managers and conservation practitioners often rely on biodiversity indicators, which are both

ecologically relevant and suitable in a funds-limited context (Lindenmayer et al., 2000). However, managers would welcome other tools capable of adequately representing variations in major biodiversity components which cannot be intensively monitored. Studying biodiversity patterns and levels of congruence between taxa is informative and can help conservation biologists design efficient tools to monitor biodiversity in a context of habitat loss and species extinctions (Gaston, 1996). Two main approaches have been put forward in this perspective (Larsson, 2001): the indirect approach uses key environmental variables, such as habitat structural complexity (Lindenmayer et al., 2000), to evaluate biodiversity levels, while the taxonomic approach uses indicator taxa whose presence and population dynamics are

\* Corresponding author at: UMR 1201 DYNAFOR, INRA, INPT, INPT-EI Purpan, Université de Toulouse, 31320, Auzeville Tolosane, France.

E-mail addresses: [laurent.larrieu@inra.fr](mailto:laurent.larrieu@inra.fr), [laurent.larrieu@crpf.fr](mailto:laurent.larrieu@crpf.fr) (L. Larrieu), [frederic.gosselin@irstea.fr](mailto:frederic.gosselin@irstea.fr) (F. Gosselin), [frederic.archaux@irstea.fr](mailto:frederic.archaux@irstea.fr) (F. Archaux), [richard.chevalier@irstea.fr](mailto:richard.chevalier@irstea.fr) (R. Chevalier), [gilles.corriol@cbnmpmp.fr](mailto:gilles.corriol@cbnmpmp.fr) (G. Corriol), [marc.deconchat@inra.fr](mailto:marc.deconchat@inra.fr) (M. Deconchat), [marion.gosselin@irstea.fr](mailto:marion.gosselin@irstea.fr) (M. Gosselin), [sylvie.ladet@inra.fr](mailto:sylvie.ladet@inra.fr) (S. Ladet), [jm.savoie@purpan.fr](mailto:jm.savoie@purpan.fr) (J.-M. Savoie), [laurent.tillon@onf.fr](mailto:laurent.tillon@onf.fr) (L. Tillon), [christophe.bouget@irstea.fr](mailto:christophe.bouget@irstea.fr) (C. Bouget).

<sup>1</sup> Deceased.

**Table 1**  
Taxonomic variables, number of plots and geographic areas with available data, and field procedures used to sample them.

Variable	Taxon and definition	Number of plots	Geographic area	Trap type or area sampled	Number of sampling years	Median plot species richness (min-max)	Total species richness
s.beetles	Saproxylc beetles	199	1, 2, 3, 4, 5, 6, 7, 8, 9, 10	1–4 Polytrap™ (window trap)	1–3	40 (5–112)	551
g.beetles	Ground beetles	136	1, 2, 3, 4, 5, 7, 10	3 or 9 Barber (pitfall trap)	1	8 (2–26)	76
bryophytes	Corticolous and saproxylc Bryophytes	142	1, 2, 3, 4, 5, 9, 10	Deadwood and living trees, 1250 m <sup>2</sup>	1	15 (2–43)	174
lichens	Corticolous macro-lichens	26	9	1 ha	1	40 (34–49)	136
bats	Bats	117	1, 2, 3, 4, 7	Ultrasound recording; 30 mn	1 (3 runs)	2 (0–13)	24
birds	Birds	119	1, 2, 3, 4, 5, 10	Point count method <a href="#">Blondel et al. (1970)</a> ; 5 mn	1 (2 runs)	11 (4–18)	58
vascular plants	Terricolous phanerogams	147	1, 2, 3, 4, 5, 9, 10	600–1018 m <sup>2</sup>	1 (1 run)	35 (9–70)	381
hoverflies	Hoverflies (Diptera Syrphidae)	11	8, 9	1 Malaise trap	2	47 (14–77)	163
polypores	Polypores s.l.	156	1, 2, 4, 7, 9, 10	0.125–0.3 ha	1–3 (1–3 total runs)	7 (1–34)	254

assumed to reflect those of other species in the community ([Landres et al., 1988](#)). The relative values of environmental variables and forest indicator taxa were reviewed by [Gao et al. in 2015](#).

Well-known and easily recordable taxa have been suggested as surrogates for lesser known or more difficult-to-record congruent taxa ([Noss, 1990](#)). Congruence between taxa can be evaluated using species richness (alpha-diversity) or composition (beta-diversity). Alpha diversity has been the most used approach to date. However, beta-diversity can provide a different pattern for cross-taxon congruence from alpha-diversity (e.g. [Cabra-Garcia et al., 2012](#)) and allows researchers to highlight processes which generate and maintain biodiversity within ecosystems ([Legendre and De Caceres 2013](#)). Unfortunately, cross-taxon congruence is generally statistically weak ([Gaston, 1996](#)) and rarely consistent ([Westgate et al., 2014](#)). Moreover, relationships between potential indicator taxa and overall biodiversity have not yet been well established ([Favreau et al., 2006](#); [Gosselin and Dallari, 2007](#); [Lindenmayer et al., 2000](#)). However, several studies have shown congruent patterns in species richness or composition, and have proposed indicator taxa in forest ecosystems ([Fensham and Streimann, 1997](#); [Kati et al., 2004](#); [Pharo et al., 1999](#); [Saetersdal et al., 2003](#)) and in agricultural ([Sauberer et al., 2004](#)) and urban contexts ([Bräuniger et al., 2010](#)). Some studies have highlighted the relevant role that a single umbrella species (e.g. [Ranius, 2002](#)) or ecosystem engineer ([Buse et al., 2008](#)) can sometimes play as an indicator in very specific conditions; however, this shortcut does not appear to be efficient in predicting the diversity of all taxa (e.g. [Sebek et al., 2012](#); [Similä et al., 2006](#)). Several reasons for this have been highlighted in the literature: (i) the wide range of behaviors ([Berger, 1997](#)) and relevant spatial scales ([Simberloff, 1998](#)) for species belonging to the same community, (ii) the absence of empirical data and evidence-based results showing the indicator function of potential indicator species ([Simberloff, 1998](#)), and (iii) contrasts in taxon ecology and therefore in their responses to environmental conditions (e.g. [Pharo et al., 1999](#)). [Brin et al. \(2009\)](#) suggested using several taxa together as bio-indicators. In this approach, it may be more efficient to use a set of non-congruent taxa, since their complementarity increases the quantity of information provided by the dataset ([Kati et al., 2004](#); [Westgate et al., 2017](#)).

In terms of cost, using a set of taxa is often more expensive since this approach requires specific methods and additional specialists to record and identify the taxa ([Nageleisen et al., 2009](#); [Puumalainen et al., 2003](#)). In a funds-limited context, partial approaches using only taxon subgroups (e.g. [Sebek et al., 2012](#)) or higher taxon levels (i.e. “taxonomic sufficiency”, [Ellis, 1985](#)), or which ignore species requiring a disproportionate detection or identification effort ([Vellend et al., 2008](#)) are promising ([Gaston, 2000](#); [Williams and Gaston, 1994](#)). Globally speaking, however, the economic feasibility of ecologically relevant indicator taxa has rarely been assessed ([Mandelik et al., 2010](#)).

This study aims to identify potential sets of indicator taxa to recommend in temperate forest biodiversity monitoring. We used previously available taxonomic data recorded at the stand level over a wide geographical area. Our dataset covers a large, contrasted forest gradient. Firstly, we quantified congruence patterns, both in terms of alpha- and beta-diversity, among nine forest taxa covering a wide range of life-history traits. Secondly, we conducted a cost-efficiency analysis of the nine forest taxa.

## 2. Materials and methods

Looking for an indicator first requires a clear definition of both the purpose ([Noss, 1990](#)) and the scale of its use ([Heink and Kowarik, 2010](#)). Our approach targets the conservation of forest species diversity, i.e. among species strictly or mainly associated with forest ecosystems. We recorded data at the stand level since that is the main operational scale for forest managers ([Failing and Gregory, 2003](#)). A wide range of forest contexts were sampled in the Atlantic and Continental zones, from lowland (plains and hills) to highland (montane and subalpine levels) forests, and in broadleaved-, mixed- and conifer-dominated stands (see Table A1 in Supplementary Material). Environmental and taxonomic data were recorded according to standardized procedures on 206 plots in ten forested geographic areas in France (Supp. Mat. Fig. A1).

### 2.1. Taxonomic data

We selected nine taxa in order to cover, *a priori*, a wide range of species behaviors and habitat requirements. Some taxa were (strictly or mainly) associated with forest, tree or woody substrates or forest-buffered climatic conditions, for example, corticolous lichens, corticolous and saproxylc bryophytes, polypores and saproxylc beetles (Table 1). Other taxa encompassed non-forest or non-tree-associated species, i.e. bats, ground beetles, birds and hoverflies. For the latter taxa, we built subsets of dendro-specialist species from the whole set of sampled species (Table 2), since dendro-specialists are more ecologically relevant and more at stake in forest conservation. In addition, for birds, subsets of forest-specific species could be less costly to inventory, since operators would be able to focus on the forest species subset instead of the whole group during sampling. However, for plants, most species are linked to open habitats (e.g. moors) and, according to most trait databases, can potentially occur along the edges or in clearings of natural forests ([Rameau et al., 1989](#); [Rameau et al., 1993](#)). Therefore we considered all the vascular plants recorded to be forest-dwelling taxa and did not build a subset of forest species for plants. Ultimately, we gathered data from two to seven taxa per plot (Supp. Mat. Table A2).

**Table 2**  
Forest specialist ecological subgroups.

Variable	Definition	References used for grouping	Median plot species richness (min-max)	Total species richness
for.g.beetles	Forest ground beetles	Desender et al. (1999); Coulon et al. (2000)	7 (2–12)	13
for.bats	Cavity- or peeling-bark-dwelling bats	Arthur and Lemaire (2009)	2 (0–9)	16
for.birds	Forest birds	Cramp (1980-94)	11 (4–18)	43
for.hover	Hoverflies (Diptera Syrphidae) with larva strictly associated with trees	Speight et al. (2013)	17 (4–25)	40

2.2. Rapid forest habitat assessment

The study stands were characterized according to the protocol for the Index of Biodiversity Potential (IBP, Larrieu and Gonin, 2008) on 1-ha circular plots centered on the sampling point used to record taxonomic data (trap or sampling area) (see Supplementary Material, tables A1 and A3 for additional information on the sampling design and the stands).

2.3. Data analysis

All calculations were performed on R v3.0.0 (R Development Core Team, 2013).

2.3.1. Checking for cross-taxon surrogates

2.3.1.1. Pairwise correlations of taxa in alpha- and beta-diversity. As recommended by Westgate et al. (2017), we simultaneously explored co-variations in alpha- and beta-diversity in the whole dataset. We focused on all the pairs of taxa for which data were available on at least 50 shared plots (Table 3). Our objective was to identify species groups whose variation in diversity could be indicative of the variation in diversity of other groups. Furthermore, we checked to see if forest-specialist subgroups co-varied differently from the full groups. We focused on small-scale spatial co-variations in species diversity, which were likely to give more robust results in the context of regional monitoring than large-scale spatial co-variations (as in e.g. Barton et al., 2015, Pierson et al., 2015). Indeed, small-scale spatial co-variations – here at the forest stand level – are more likely to be free of biogeographic co-variations than large-scale ones – here, whole forest

estates – and therefore be more related to temporal co-variations or variations related to management actions (Bunnell and Huggard, 1999).

Beta-diversity congruence between taxa was assessed using the Procrustes rotation on NMDS ordination of Jaccard dissimilarity matrices for occurrence data (Peres-Neto and Jackson, 2001). Permutation tests associated to the Procrustes method (*protest* function, R-package *vegan*, number of runs = 1.000) can reveal the non-randomness of the congruence in fit between multivariate data tables regarding homologous observations (taxon pairs on sampling sites), using the  $m^2$  Procrustes statistic. In order to account for the nested structure of our dataset, permutations were conditioned upon geographic area, which was a stratifying variable.

For alpha-diversity, we first modeled the species richness data through a Poisson generalized linear mixed model (R-package *lme4*) with the species richness of the studied groups as a function of the interaction between taxonomic group and geographic area (to remove the effect of geographic area) and with a random plot effect per taxonomic group (to account for potential over-dispersion). Based on this model, we then transformed the original species richness into residuals which represented variations in species richness freed from geographic area effects and whose probability distribution was standardized. To do this, we used randomized quantile residuals (Dunn and Smyth 1996) that took into account these fixed effects as well as the marginal distribution of plot random effects for each taxonomic group (much as in Millar 2009). Indeed, for reasons similar to those in Millar (2009), we believe that such residuals are better estimated by integrating them on top of the distribution of random effects rather than by using the “optimal” random-effect estimator. This gave us a novel kind of residual: marginalized randomized quantile residuals, which we then transformed

**Table 3**  
Number of plots sharing at least two taxa; in bold, co-occurrences in over 50 plots; g.beetles = ground beetles, s.beetles = saproxylic beetles.

Taxons	bryophytes	g.beetles	bats	s.beetles	vascular plants	lichens	polypores	birds
g.beetles	<b>84</b>							
bats	<b>90</b>	<b>83</b>						
s.beetles	<b>135</b>	<b>132</b>	<b>113</b>					
vascular plants	<b>108</b>	<b>117</b>	<b>87</b>	<b>140</b>				
lichens	22	0	0	23	<b>52</b>			
polypores	<b>128</b>	<b>94</b>	<b>105</b>	<b>156</b>	<b>124</b>	<b>52</b>		
birds	<b>84</b>	<b>115</b>	<b>85</b>	<b>116</b>	<b>119</b>	0	<b>96</b>	
hoverflies	8	0	0	9	8	8	9	0

into a Gaussian scale through the quantile Gaussian standard distribution, yielding normalized marginalized randomized quantile residuals. We then performed Pearson correlation coefficient tests (*cor* and *cor.test* functions, R-package *stats*) on these residuals for each pair of taxa.

For both alpha and beta-diversity, we also estimated the statistical significance of pairwise taxon correlations with p-values adjusted to account for multiple comparisons (Rice 1989). As suggested by Moran (2003), we added two overall tests of the significance of the number of tests found to be significant to the  $p < 0.05$  and  $p < 0.01$  levels without multiple comparison correction. Indeed, individual tests might all be rendered insignificant by multiple test correction, while the total number of significant tests could be quite high compared to what would be expected under the null hypothesis. These overall tests for the total number of significant tests were based on the hypothesis that individual tests are independent of each other (as in Moran 2003). We corrected the test by applying a randomization for the count of significant tests as in Gosselin (2011): if  $n$  is the number of significant tests with  $p < \alpha$  over  $N$ , the p-value of this overall test is based on the binomial probability distribution with parameters  $\alpha$  and  $N$ , and is calculated as the sum of the cumulative probability between 0 and  $n-1$ , and a random uniform number between 0 and 1 multiplied by the probability of  $n$ . This calculation allowed us to obtain a uniform distribution for the ensuing p-value under the null model. We used two reference p-values in order to analyze the number of significant tests at a usual level of significance (0.05) as well as at a more stringent level (0.01).

**2.3.1.2. A single taxon as a surrogate for the full set of the other taxa?** We looked for surrogates of overall alpha- and beta-diversity, i.e. whether the species richness of a given taxon was a surrogate for the total species richness of all the other taxa combined, or whether the beta-diversity for a given taxon was a surrogate of the beta-diversity for all the other taxa. Since we used previously available taxonomic datasets, the data were unbalanced; not all the taxa were recorded on each of the 206 plots. Even so, twenty-five combinations of two to seven taxa among the nine targeted taxa were still available (Supp. Mat. Table A4). Among the 25 combinations, we selected the combination that gave us the best trade-off between the total number of plots and the number of shared taxa. Four taxa (namely ground beetles, saproxylic beetles, birds and vascular plants) had been systematically sampled together on 112 plots (Supp. Mat. Table A4 and Fig. A2) and were retained for further analyses. We performed Pearson correlation coefficient tests between the species richness of each taxon and the total species richness of the set of the other three taxa. Then, we performed Procrustes analyses (see above) on dissimilarity matrices based on each taxon and on the three other taxa (with permutation tests conditioned on geographic area). Due to the limited number of cases being compared, no multiple comparison correction was applied to the tests.

### 2.3.2. Effectiveness of single- or multi-taxon subsets for total richness assessment and plot ranking

For the same selection of 112 plots and four taxa, we compared the species richness ranking of the plots based on the whole four-taxon assemblage with single-, two- and three-taxon subsets only. We calculated the difference in rank between the whole assemblage and the taxon subsets at the plot level, then calculated the mean rank difference in absolute values. Confidence intervals (95%) of mean difference were bootstrap estimated (1000 replicates). We also calculated the simple contribution of single- or multi-taxon subsets (in terms of mean and of variation) to total species richness.

## 2.4. Cost-efficiency of potential indicator taxa

In order to assess the cost-efficiency of potential indicator taxa, we analyzed their “sampling cost” and their performance score (sensu Heink and Kowarik 2010).

First, a composite sampling cost was assessed for each taxon,

accounting for several criteria: labor, material purchase price and technical and logistic constraints (see Table A5 in Supp. Mat. for the cost classes we used). We enlisted the expertise of 12 taxonomists to help us quantify nine variables: (i) *cost of sampling devices* (e.g. traps), (ii) *cost of initial field sampling*, (iii) *cost of intra-annual replicates*, (iv) *estimated gain on record completeness* when sampling is repeated (e.g. to take into account the variability of climatic conditions or insect flight seasons), (v) *complexity of taxonomic identification*, (vi) *availability of taxonomic experts* (in France), (vii) *availability of documents* for species identification and taxonomic references, (viii) *laboratory costs* for species identification, and (ix) *time required after sampling* to obtain the data when laboratory work is required. Taxon scores were averaged at the criterion level when several experts gave different values for the same criterion.

To evaluate the performance score of each taxon, we divided the 20 criteria reviewed by Heink and Kowarik (2010) into five sets. The first set, *Feasibility for analysis and interpretation*, encompassed five criteria: (i) *level of taxonomic knowledge*, (ii) *availability of databases* for life-history traits, (iii) *portability*, incl. detectability (i.e. availability of standard sampling methods and calibrated protocols), (iv) *suitability for statistical analysis* (i.e. possibility of large sample sizes and low random variations), and (v) *availability of reference values*. The second set, *Efficiency*, encompassed three criteria: (i) *universality* (i.e. broad geographical range and many macro-habitats covered), (ii) *parsimony* (i.e. possibility to reduce the number of items observed with minimal loss of information), and (iii) *taxonomic sufficiency* (i.e. relevance of using higher-taxon levels, e.g. the number of genera or families as surrogates of species richness). The third set, *Relationship between indicator and indicanda*, encompassed two criteria: (i) *empirical level of correlation between indicator and indicanda* for both species composition and species richness (Table 4 – yielding two scores for each taxon – forest sub-groups not considered), based on the percentages of tested taxa shown to be significantly correlated ( $p < 0.05$ ) with the indicator-taxon in our global covariation matrices, and (ii) *aggregation of ecological information* (i.e. ecological breadth depicting the amount of unmeasured biodiversity parameters correlated with the taxon). The fourth set, *Ecological information provided by the indicator*, encompassed six criteria: (i) *relevance*, referring to how relevant the indicator is to stakeholder interests (e.g. obvious ecosystemic services), (ii) *sensitivity to environmental change* (i.e. the speed and intensity of the response of the taxon to habitat change) (iii) *habitat specialization and dependence* on environmental conditions, (iv) *functional importance* for the ecosystem, (v) *distinction between natural and managed forests* and (vi) *rarity of and threat to the taxon* in managed forests. Finally, the fifth set, *Stakeholder perception*, encompassed three criteria: (i) *acceptance of norms* for taxon conservation, (ii) *easy depiction and comprehensibility* of the taxon’s role in forest ecosystems, and (iii) *economic importance* (whatever the direction of the effect, i.e. positive or negative, for stakeholders). Thus, one criterion, encompassing two scores, was evaluated by using the results of this study. For the other 19 criteria, the score given to each criterion was based on the expert judgment of a subset of eight taxonomists among the 12 consulted for evaluation of the sampling effort. Taxonomic experts attributed a score for each qualitative criterion as follows: 10 = low, 20 = medium, 30 = high. One of the authors (LL) coordinated the scoring to avoid misinterpreting the variables, to standardize the way the scores were attributed and decide in case of disagreement between experts. The sum of the scores for the 20 criteria was used as a performance score for each taxon. Scores ranged from 9 to 33 for sampling costs and from 180 to 740 for performance.

## 3. Results

### 3.1. Cross-taxon surrogates

#### 3.1.1. Pairwise correlations of taxa in alpha- and beta- diversity

We found four significant pairwise co-variations in alpha-diversity

**Table 4**

Pairwise correlations of taxa in alpha- and beta-diversity without multitest correction; alpha-diversity below the diagonal: Pearson coefficients based on normalized marginalized randomized quantile model residuals; beta-diversity above the diagonal: Procrustes analysis of the congruence in fit between dissimilarity matrices (with permutation tests conditioned on the geographic area); significance of relationships: \*\*\*:  $p < 0.001$ ; \*\*:  $0.001 < p < 0.01$ ; \*:  $0.01 < p < 0.05$ ; ns:  $p > 0.05$ ; g.beetles = ground beetles, s.beetles = saproxylic beetles, for = forest subgroup; NA = data not available; NT = not tested; nc = not computed since taxa co-occurred in less than 50 plots. Significance levels indicated are for individual tests. After correcting for multiple comparisons at the  $p < 0.05$  level, we found no significant tests for alpha-diversity, and only two significant results for beta-diversity (between vascular plants and ground beetles, and vascular plants and bryophytes).

Taxa	bryophytes	g.beetles	for.g.beetles	bats	for.bats	s.beetles	vascular plants	lichens	polypores	birds	for.birds
bryophytes		0.711 <sup>ns</sup>	0.602 <sup>ns</sup>	0.490 <sup>ns</sup>	0.474 <sup>ns</sup>	0.783 <sup>ns</sup>	0.599 <sup>***</sup>	nc	0.509*	0.395 <sup>ns</sup>	0.398 <sup>ns</sup>
g.beetles	-0.16 <sup>ns</sup>		NT	0.299 <sup>ns</sup>	0.299 <sup>ns</sup>	0.559**	0.525**	NA	0.419 <sup>ns</sup>	0.308 <sup>ns</sup>	0.578 <sup>ns</sup>
for.g.beetles	0.18 <sup>ns</sup>	NT		0.240 <sup>ns</sup>	0.147 <sup>ns</sup>	0.409 <sup>ns</sup>	0.635 <sup>ns</sup>	NA	0.313 <sup>ns</sup>	0.573 <sup>ns</sup>	0.491 <sup>ns</sup>
bats	0.24*	-0.34**	-0.12 <sup>ns</sup>		NT	0.272 <sup>ns</sup>	0.577 <sup>ns</sup>	NA	0.308 <sup>ns</sup>	0.071 <sup>ns</sup>	0.034 <sup>ns</sup>
for.bats	0.19 <sup>ns</sup>	-0.21 <sup>ns</sup>	-0.1 <sup>ns</sup>	NT		0.282 <sup>ns</sup>	0.393 <sup>ns</sup>	NA	0.306 <sup>ns</sup>	0.157 <sup>ns</sup>	0.205 <sup>ns</sup>
s.beetles	0.04 <sup>ns</sup>	0.17*	0.06 <sup>ns</sup>	0.16 <sup>ns</sup>	0.18 <sup>ns</sup>		0.471 <sup>ns</sup>	nc	0.501*	0.483 <sup>ns</sup>	0.450 <sup>ns</sup>
vascular plants	0.13 <sup>ns</sup>	0.15 <sup>ns</sup>	0 <sup>ns</sup>	0.09 <sup>ns</sup>	-0.04 <sup>ns</sup>	0.15 <sup>ns</sup>		0.479**	0.493 <sup>ns</sup>	0.489 <sup>ns</sup>	0.604*
lichens	nc	NA	NA	NA	NA	nc	-0.02 <sup>ns</sup>		0.340 <sup>ns</sup>	NT	NT
polypores	0.22*	-0.17 <sup>ns</sup>	-0.02 <sup>ns</sup>	-0.02 <sup>ns</sup>	0.01 <sup>ns</sup>	0.1 <sup>ns</sup>	0.07 <sup>ns</sup>	0 <sup>ns</sup>		0.331 <sup>ns</sup>	0.300 <sup>ns</sup>
birds	0.04 <sup>ns</sup>	0.11 <sup>ns</sup>	0.06 <sup>ns</sup>	0.19 <sup>ns</sup>	0.17 <sup>ns</sup>	0.16 <sup>ns</sup>	-0.04 <sup>ns</sup>	NA	0.16 <sup>ns</sup>		NT
for.birds	0.03 <sup>ns</sup>	0.08 <sup>ns</sup>	0.07 <sup>ns</sup>	0.19 <sup>ns</sup>	0.15 <sup>ns</sup>	0.13 <sup>ns</sup>	-0.06 <sup>ns</sup>	NA	0.19 <sup>ns</sup>	NT	

representing roughly 9% of the tested taxon pairs (see Table 4 below the diagonal; co-variation direction indicated in brackets): bats with bryophytes (+) and ground beetles (-), saproxylic beetles with ground beetles (+), polypores with bryophytes (+). All significant co-variations were weak (Pearson < 0.34). We found six significant pairwise co-variations in beta-diversity representing roughly 14% of the tested taxon pairs (see Table 4 above the diagonal): (i) vascular plants with bryophytes, ground beetles, lichens and forest birds, (ii) saproxylic beetles with ground beetles, and (iii) polypores with bryophytes.

After correcting for multiple comparisons, we found no significant tests (at the  $p < 0.05$  level) for alpha-diversity, and only two significant results (between vascular plants and ground beetles, and vascular plants and bryophytes) for beta-diversity. When we then tested the significance of the number of significant tests, we found that the number of tests for alpha-diversity significant at  $p < 0.05$  was not surprising (at  $p < 0.05$ ), while the number of tests for beta-diversity significant at  $p < 0.05$  and  $p < 0.01$  were very surprising (respectively  $p < 0.01$  and  $p < 0.001$ ).

3.1.2. A single taxon as a surrogate for the full set of other taxa?

At the plot level (and for the selection of 112 plots), median (and range of) values for alpha diversity of saproxylic beetles, birds, vascular plants and ground beetles were 33 (5–69), 15 (4–27), 35 (9–70) and 9 (2–35) species, respectively. The alpha diversity of saproxylic beetles, birds, vascular plants or ground beetles alone was a good surrogate for the alpha diversity of the other taxa since all the Pearson correlations were significant and showed high values for saproxylic beetles and vascular plants (Table 5). For saproxylic beetles only, we measured a significant correlation between inter-plot distance matrices based on each single taxon and the matrix based on the three other taxa pooled together.

3.1.3. Single- or multi-taxon subsets as surrogates for a whole set of taxa to determine plot ranking

At the single-, two- and three-taxon level, respectively (Table 6), vascular plants, the combination of saproxylic beetles and vascular

**Table 5**

Pearson correlations based on model residuals and Procrustes analysis of the congruence in fit between dissimilarity matrices (with permutation tests conditioned on the geographic area) for each taxon used as an indicator for (i) species richness (SR) or (ii) variation in species composition of the cumulative set of the three other taxa; \*\*\*:  $p < 0.001$ ; \*\*:  $0.001 < p < 0.01$ .

	Pearson correlation coefficient (SR)	Procrustes statistic (matrix dissimilarities)	% of total species richness (average at the plot level)
saproxylic beetles	0.651 <sup>***</sup>	0.523*	36.4
birds	0.472 <sup>***</sup>	0.487 <sup>ns</sup>	17.3
vascular plants	0.743 <sup>***</sup>	0.516 <sup>ns</sup>	37.5
ground beetles	0.332 <sup>***</sup>	0.525 <sup>ns</sup>	8.8

plants, and the combination of saproxylic beetles, vascular plants and birds displayed the highest average contribution to total species richness. Birds and ground beetles had the lowest average and the most variable contribution to total species richness. Moreover, the higher the average contribution to total species richness, the lower the mean rank difference between the richness ranks based on the whole assemblage and the richness ranks based on a single-taxon subset.

In order to rank plots on the basis of their species richness, we identified four groups of taxon subsets (noted a, b, c and d in Table 6). As expected, the best combination to rank plots was saproxylic beetles + vascular plants + birds, i.e. the three-taxon set cumulating the highest proportion of all species. Nonetheless, in the third performance group (significant group c in Table 6), selecting only saproxylic beetles had a ranking performance equivalent to the vascular plants + birds + ground beetle association.

3.2. Taxon cost efficiency

Based on their experiential knowledge, the taxonomic specialists we consulted classified birds and vascular plants as the cheapest taxa to

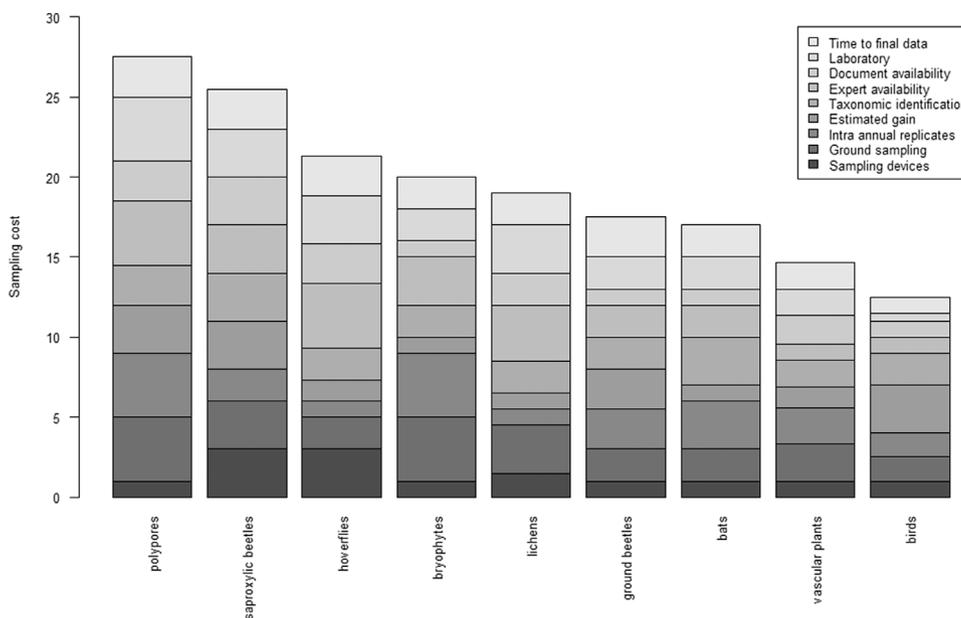
**Table 6**

Contribution to total species richness and differences in plot ranking of single-, two- and three-taxon subsets as compared with the full four-taxon assemblage; g.beetles = ground beetles, s.beetles = saproxylic beetles; letters a, b, c and d indicate significant groups of combinations based on bootstrap CI.

	Contribution to total species richness		Plot ranking	
	Mean (%)	Relative standard deviation (%)	mean rank difference (absolute values)	bootstrap CI
s.beetles_vascular plants_birds	91.24	3.42	0.66 <sup>a</sup>	0.49–0.86
s.beetles_vascular plants_g.beetles	82.69	7.16	5.25 <sup>b</sup>	4.38–6.44
s.beetles_vascular plants	73.92	10.04	5.54 <sup>b</sup>	4.54–6.74
vascular plants_birds_g.beetles	63.56	16.80	16.91 <sup>c</sup>	14.23–19.56
s.beetles_birds_g.beetles	62.52	16.43	16.38 <sup>c</sup>	14.18–18.86
vascular plants_birds	54.80	19.99	16.91 <sup>c</sup>	14.65–20.01
s.beetles_birds	53.75	17.58	16.59 <sup>c</sup>	13.89–19.07
vascular plants_g.beetles	46.25	20.43	18.71 <sup>c</sup>	15.96–22.19
s.beetles_g.beetles	45.20	24.23	18.95 <sup>c</sup>	16.09–21.91
vascular plants	37.48	27.41	18.55 <sup>c</sup>	15.70–21.69
s.beetles	36.44	29.30	18.55 <sup>c</sup>	15.75–21.49
birds_g.beetles	26.08	28.46	29.54 <sup>d</sup>	26.20–33.33
birds	17.31	34.21	29.68 <sup>d</sup>	26.47–33.73
g.beetles	8.76	35.64	33.39 <sup>d</sup>	29.30–38.29

study, while polypores and saproxylic beetles were the most expensive (Fig. 1; see details of the scores in Supp. Mat. Table A5). Saproxylic beetles and hoverflies require expensive sampling devices (window and Malaise traps) because of their relatively short life-spans.

Considering the relationship between sampling cost (Supp. Mat. Table A5) and performance score (Supp. mat. Table A6), we distinguished four categories of taxa based on medians (Fig. 2): (i) low-cost (12.5–14.7 points) yet effective (390–467 points) with vascular plants and birds; (ii) low-cost (17–17.5) but ineffective (333–340) with ground beetles and bats; (iii) costly (27.5–27.5) yet effective (403–440) with polypores and saproxylic beetles; and (iv) both costly (20) and ineffective (366) with bryophytes. In addition to these categories, lichens showed an average sampling cost (19) and a weak performance (350). Finally, hoverflies were costly (21.3) and showed an average



**Fig. 1.** Sampling cost estimated by 12 taxonomist experts for 9 taxa based on 9 criteria; scores by taxon were averaged when several experts gave different values; potential total score range = 9–33.

performance (380), but they were only partially evaluated for performance since, in our sample, they did not share enough plots with the other taxa to perform congruence analyses.

**4. Discussion**

Seeking biodiversity indicators has a rather long history (see e.g. Murdoch et al., 1972). Conservation strategies often rely on surrogates (called umbrella, keystone or target species), according to the recommendations of e.g. Mills et al. (1993) or Lambeck (1997), and assume significant benefits for biodiversity (Caro 2010). However, the performance of these indicator species has rarely been tested. Among the nine taxa assessed in this study, only birds and vascular plants had been regularly evaluated before 2006 (Wolters et al., 2006). Since then, several studies have looked at bryophytes, fungi and lichens (e.g. Bagella 2014; Mysak and Horsak, 2014; Santi et al., 2010; Rooney and Azeria, 2015) but fungi has ultimately been poorly studied to date (Westgate et al., 2017).

**4.1. An analytical approach to avoid potential pitfalls in the evaluation of cross-taxon congruence**

Most published results related to cross-taxon congruence did not take into account the spatial structure revealed by the data (e.g. simple correlation coefficients on raw data as in Lovell et al., 2007; Negi and Gadgil, 2002 or Ricketts et al., 2002; but see Sabatini et al., 2016). We compared the pairwise correlations of taxa for alpha- and beta-diversity in models accounting for the spatial pattern of our sampling design and in models which did not account for spatial patterns (Suppl. Mat., Fig. A3 and Table A7). We found that, in terms of average magnitude, the correlation was not strongly affected when the spatial configuration of the plots was accounted for; the Pearson values were only slightly lower than the Pearson values on standardized residuals. However, values were much less extreme than for uncorrected residuals (Fig. A3, Suppl. Mat). In terms of significance, 39% and 82% of the statistical decisions in alpha and beta-diversity, respectively, were changed (rejecting or accepting the null hypothesis) for pairwise correlations. Results were mostly less significant for the spatially corrected results: about 34% of the pairwise correlations in alpha-diversity (resp. 68% for beta-diversity) were actually changed from significant to non-significant, with an additional 12% for beta-diversity that shifted to a less significant result (Suppl. Mat. Table A7). These rough metrics clearly demonstrate

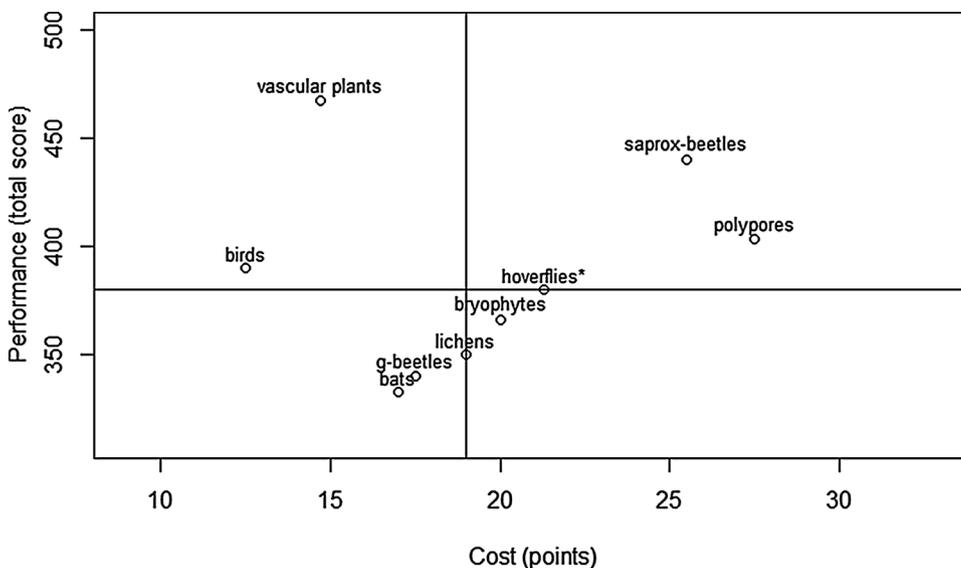


Fig. 2. Sampling cost and performance score for nine potential bio-indicator taxa; potential score ranges: 9–33 points for cost, 180–740 points for performance; lines split the figure according to median scores; \*: the performance score of hoverflies may be under-evaluated (max 200 points) due to untested relationships with the other taxa (number of plots shared < 50); see Material and Methods section for more explanation about constructing the sampling cost and performance score; g-beetles = ground beetles, saprox-beetles = saproxylic beetles.

that our results concerning cross-taxon surrogacy changed considerably when we accounted for the spatial pattern of the sampling design, both for alpha- and beta-diversity, and not only for alpha-diversity as in Westgate et al. (2017).

We also compared the statistical significance of pairwise taxon correlations in alpha- and beta-diversity with or without p-value adjustments to account for, or not to account for, multiple comparisons (Suppl. Mat. Table A8). Logically, the results were much less significant after this adjustment: after adjusting p-values, about 9% of the statistical decisions in alpha and beta-diversity were changed from significant to non-significant (i.e. accepting the null hypothesis) for pairwise correlations. Moreover, 5% of the pairwise correlations in beta-diversity became less significant (Suppl. Mat. Table A8). Overall, with this multiple test correction, we found no significant tests (at the  $p < 0.05$  level) for alpha-diversity, and only two significant results for beta-diversity. This p-value adjustment was designed to maintain enough power – compared to the Bonferroni technique – to correctly reject the null hypothesis for individual tests, thus reducing the likelihood of false positives (type I errors) for the entire set of tests by taking into consideration the number of comparisons being made (Rice, 1989). Applying this alternative statistical approach for multiple testing led us to accept the null hypothesis more often, i.e. to decrease Type I errors of individual tests. Based on Moran (2003), we finally decided to keep both pieces of information in Table 4 and to interpret the significant results in Table 4 with great circumspection.

#### 4.2. The use of taxon surrogacy for beta- vs alpha-diversity to define biodiversity indicators

We found more pairwise co-variations in beta- than in alpha-diversity (6 vs 4). Species richness is a univariate value which is easier to use than species composition in routine calculations (Magurran, 2004). This may explain why cross-taxon congruence through variations in beta diversity has rarely been studied. Furthermore, the few published results regarding this issue are contrasted (e.g. Mandelik et al., 2012; Negi and Gadgil, 2002). Prendergast (1997), Bilton et al. (2006) and Gaspar et al. (2010) found more inconsistency between species richness than between species composition across taxa and sites, and therefore suggested using beta-diversity rather than alpha-diversity to select surrogate taxa. Nordén et al. (2007) and Lovell et al. (2007) had already suggested complementing species richness data with species composition data, especially in heterogeneous habitats where the use of species richness to identify congruent relationships may lead to misinterpretation (Lovell et al., 2007). Westgate et al. (2017) highlighted

that congruence in beta-diversity is more robust than congruence in alpha-diversity to avoid study-related effects. Researchers should further explore using covariations in beta diversity, in addition to or instead of co-variations in alpha-diversity, to define biodiversity indicators.

#### 4.3. Cross-taxon congruence

In our study, vascular plants were the taxon the most congruent with the other taxa tested for beta-diversity, while bryophytes, bats and ground beetles were the most congruent taxa for alpha-diversity. However, it should be underlined that the observed covariations were weak and no single taxon was firmly identified as a relevant surrogate for the other taxa. Our approach highlights that the choice of the particular statistical method used (i.e. with or without removal of macro spatial structure, with or without multiple test correction) strongly influences the level of correlation and the significance of results. This might partly explain variations in past results and calls for a greater attention to these statistical issues (in line with Biggs et al., 2009). Most studies have found weak cross-taxon congruence (e.g. Grand et al., 2004; Lovell et al., 2007; Negi and Gadgil, 2002; Ricketts et al., 2002). Prendergast et al. (1993), Lombard (1995), Oliver and Beattie (1996), Kerr (1997), Kati et al. (2004) and, in a review, Wolters et al. (2006) concluded that no taxon has as yet proved to be universal (in accordance with Nordén et al., 2007) or even to be a good predictor for the species richness of other taxa. However, Pharo et al. (1999) found that vascular plants were robust surrogates for beta-diversity. Moreover, some studies deemed vascular plants to be relevant surrogates for alpha-diversity: Fensham and Streimann (1997) in forests, Sauberer et al. (2004) in agricultural landscapes and Bräuniger et al. (2010) in urban contexts. In line with Duan et al. (2016), we highlighted a significant congruence between assemblages of vascular plants and ground beetles. Delayed responses could also influence cross-taxon congruence. Different patterns in a species' delayed responses to habitat change – i.e. extinction debt or colonization credits – have previously been highlighted for hoverflies (Bommarco et al., 2014; Herrault et al., 2016), vascular plants (Bommarco et al., 2014) and birds (Ford et al., 2009).

Some well-known – even emblematic – mammals and birds have been used as biodiversity surrogates (Wolters et al., 2006). However, Landres et al. (1988) and Fattorini (2010) warned against the use of vertebrate surrogates to assess habitat suitability for other species, or to make conservation decisions. Eglington et al. (2012) found that, in temperate regions, bird species richness only moderately reflected the

species richness of vascular plants and other animal taxa, even though in Italian forests at the stand scale, birds were shown to be effective surrogates for vascular plants (Blasi et al., 2010; Santi et al., 2010). In our forest data, the correlations in alpha diversity between birds and the other tested taxa were never significant. However, our estimates for bird richness were probably too low and, as importantly, rather imprecise, due to the short duration (total of 10 min per plot, in line with e.g. Bonthoux and Balent, 2012) of our bird point counts (see Drapeau et al., 1999); this may at least partly explain the poor indicator value we found for birds. In addition, we found no significant co-variations in beta-diversity between birds and other taxa. Using a meta-analysis approach covering a wide range of ecosystems and taxa, Westgate et al. (2017) highlighted that vascular plants and birds outperform other taxa as surrogates for both alpha- and beta-diversity.

Surrogacy was expected to be higher when ecological overlap occurred between the target and surrogate taxa. Similar responses to environmental gradients and ecological relationships between taxa generally lead to strong congruence (Gaspar et al., 2010). For instance, we may assume that congruence between the saproxylic taxa is strong (see e.g. Jonsson and Jonsell, 1999). Our results did not actually allow us to illustrate these assumed relationships; no single taxon unequivocally proved to be a saproxylic surrogate. This may be due to the large within-group heterogeneity in habitat preferences (e.g. preference for abiotic conditions) among saproxylic organisms. For instance, let us take bryophytes and saproxylic beetles. Most bryophytes require deadwood resources in shady contexts because they need humidity to reproduce (Jahns, 1989), while the variety of saproxylic beetles species recorded through window trapping increased with stand openness (Bouget et al., 2014). This corresponds to their multi-habitat behavior (beetle larvae need saproxylic substrates while most imagoes are floricolous) and the positive effect of higher temperature on their activity.

Contrary to expectations, subsets of forest species did not have higher surrogacy in either beta- or alpha-diversity than the whole taxon including generalist – sometimes it was even lower.

#### 4.4. Cost-efficiency of taxa

Very few studies have actually evaluated the cost-efficiency of using a wide range of taxa to enhance surrogacy (see Gardner et al., 2008; Mandelik et al., 2010). Thanks to both empirical expert knowledge and the results from our study, we highlight four categories of taxa in terms of cost-efficiency, from low-cost but ineffective to costly but effective. Several individual taxa are commented on below.

First, we found vascular plants to be a very efficient taxon, probably because tree species are included in the group. Including trees actually improves the score for vascular plants on several criteria, such as *Relevance for stakeholder interests*, *Functional importance*, *Easy depiction and comprehensibility of the role of the taxon* or *Economic importance*. Using other criteria relative to the key attributes of forest ecosystems, e.g. maturity gradient, would decrease the performance score of vascular plants. Furthermore, vascular plant species richness is very sensitive to the nutrient-richness of the soil (e.g. Rameau et al., 1993). Since our sample included a very low proportion of sites with very nutrient-poor soils such as podzols, the mean contribution of vascular plants to both total species richness and plot ranking may have been over-estimated.

Secondly, saproxylic beetles were classified as an effective but costly group. It should be pointed out, however, that the growing use of faster innovative sampling methods, such as DNA meta-barcoding or environmental DNA analysis, should dramatically reduce the effort required for saproxylic beetles (Bohmann et al., 2014). Meta-barcoding has recently been used to successfully assess arthropod diversity (e.g. Yu et al., 2012). In the future, barcoding could be relevant for other taxa as well, such as polypores which are currently directly sampled from decayed wood at great cost (see e.g. Runnel et al., 2015). Surrogacy correlations in alpha- and beta-diversity values for saproxylic

species between taxa sampled with classical (insect trapping, sporocarp inventory...) and molecular (NGS) methods are under study (e.g. Ovaskainen et al., 2013).

Thirdly, in order to give a benchmark for cost-efficiency, we include a cost analysis for hoverflies, which have already been used as an indicator taxon at the landscape scale (Sommaggio and Burgio, 2003), even though our dataset did not enable us to test their cross-taxa congruence.

Fourthly, even though ground beetles have been recommended as relevant surrogates in terrestrial environmental evaluations (Gerlach et al., 2013), we found their performance rather weak in forest conditions; they were also poor indicators of forest plot ranking.

Some performance criteria, particularly *Aggregation of ecological information*, *Sensitivity to environmental change* and *Functional importance for the ecosystem*, could have been under-evaluated in our results since only a few studies were available to provide empirical data and make the expert judgment more robust. For these three criteria grouped together, the performance scores could have been underestimated by: (i) 20 points for vascular plants (i.e. 4% of the current score) and hoverflies (5%), (ii) 30 points for bryophytes (8%), polypores (7%) and saproxylic beetles (7%), (iii) 40 points for lichens (11%) and birds (10%), (iv) 50 points for ground beetles (15%), and (v) 60 points for bats (18%).

#### 4.5. Complementarity of taxa: toward a multi-taxon set of indicators?

Our results showed that using a set of two or three taxa, as opposed to single-taxon approaches, drastically increased surrogacy effectiveness, in accordance with Jonsson and Jonsell (1999), Kati et al. (2004) and Gerlach et al. (2013). Associating saproxylic beetles with vascular plants, or with both vascular plants and forest birds, seemed to be the most cost-efficient, considering both the set's indicator power and its sampling cost. Furthermore, these three taxa (vascular plants, saproxylic beetles and birds) showed low congruence in alpha-diversity and therefore provided complementary information. In Mediterranean ecosystems, Mandelik et al. (2010) also suggested using a combination of plants and insects to improve surrogacy in biodiversity monitoring. Furthermore, Gerlach et al. (2013) recommended associating taxa from contrasting trophic guilds covering a wide gradient of dispersal abilities.

## 5. Conclusion and research perspectives

For indicator taxa to be routinely used as tools for evaluating, monitoring and decision-making, managers need to consider the trade-offs between their performance and sampling costs (Gardner et al., 2008). This paper clarifies the cost-efficiency of nine potential forest indicator taxa and their combinations. In a companion paper under preparation, we will address the relationships between indicator taxa and key environmental variables for sets of forest biodiversity indicators. It should be noted that our dataset includes taxa and environmental variables measured at the local stand scale; however, the strength of the correlation between taxon species richness of taxa is known to be scale-dependent (Eglington et al., 2012; Jonsson and Jonsell, 1999; Santi et al., 2016). Moreover, most of our data is related to single-year sampling (Table 1) and this short-term temporal scale did not allow us to take into account community dynamics and changes in patterns over time (Favreau et al., 2006). Therefore, further research should consider larger spatial and temporal scales, i.e. congruence of taxa in the long-term and at the landscape scale. In addition, further research should also consider the intensity of human disturbance and its impact on congruence results (Rooney and Azeria, 2015).

## Acknowledgements

This research was funded by the French Ministry in charge of the

Ecology through the “Biodiversité, Gestion Forestière et Politiques Publiques” (BGF) program (convention 10-MBGD-BGF-1-CVS-092, n°CHORUS 2100 214 651). Part of this work was funded by the French Environment and Energy Management Agency (ADEME), and European (FEDER) and French grants (Conseil Regional de Midi-Pyrénées).

We are indebted to B. Nusillard, A. Lassauce, Y. Paillet, C. Moliard (Irstea), T. Barnouin, T. Noblecourt, F. Soldati, H. Voiry (ONF), A. Brin, H. Brustel, L. Valladares (EIP), J. Willm, L. Burnel (INRA), J.P. Sarthou (INRA), V. Sarthou (Syrphys), F. Prud'homme and all the local forest managers (private and public, from ONF and RNF) for their field and laboratory work, access to databases or their expert analysis of cost effectiveness, to V. Moore who reviewed the English manuscript and to the two reviewers who provided insightful comments that helped improve the manuscript.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.ecolind.2017.12.044>.

## References

- Arthur, L., Lemaire, M., 2009. Les chauves-souris de France, Belgique, Luxembourg et Suisse Biotope, Mèze (collection Parthénope). MNHN, Paris.
- Bagella, S., 2014. Does cross-taxon analysis show similarity in diversity patterns between vascular plants and bryophytes? Some answers from a literature review. *C. R. Biol.* 337 (4), 276–282.
- Barton, P.S., Pierson, J.C., Westgate, M.J., Lane, P.W., Lindenmayer, D.B., 2015. Learning from clinical medicine to improve the use of surrogates in ecology. *Oikos* 124 (4), 391–398.
- Berger, J., 1997. Population constraints associated with the use of black rhinos as an umbrella species for desert herbivores. *Conserv. Biol.* 11, 69–78.
- Biggs, R., Carpenter, S.R., Brock, W.A., 2009. Spurious certainty: how ignoring measurement error and environmental heterogeneity may contribute to environmental controversies. *Bioscience* 59, 65–76.
- Bilton, D.T., Mcabendroth, L., Bedford, A., Ramsay, P.M., 2006. How wide to cast the net? Cross-taxon congruence of species richness, community similarity and indicator taxa in ponds. *Freshwater Biology* 51, 578–590.
- Blasi, C., Marchetti, M., Chiavetta, U., Aleffi, M., Audisio, P., Azzella, M.M., Brunialti, G., Capotorti, G., Del Vico, E., Lattanzi, E., Persiani, A.M., Ravera, S., Tilia, A., Burrascano, S., 2010. Multi-taxon and forest structure sampling for identification of indicators and monitoring of old-growth forest. *Plant Biosyst.* 144 (1), 160–170.
- Blondel, J., Ferry, C., Prochot, B., 1970. La méthode Des Indices Ponctuels d'abondance I.P.A Ou Des Relevés d'Avifaune Par Points d'écoute 38. *Alauda*, pp. 55–71.
- Bohmann, K., Evans, A., Gilbert, M.T.P., Carvalho, G.R., Creer, S., Knapp, M., Yu, D.W., de Bruyn, M., 2014. Environmental DNA for wildlife biology and biodiversity monitoring. *Trends Ecol. Evol.* 29, 358–367.
- Bommarco, R., Lindborg, R., Marini, L., Oeckinger, E., 2014. Extinction debt for plants and flower-visiting insects in landscapes with contrasting land use history. *Divers. Distrib.* 20, 591–599.
- Bonthoux, S., Balent, G., 2012. Point count duration: five minutes are usually sufficient to model the distribution of bird species and to study the structure of communities for a French landscape. *J. Ornithol.* 153 (2), 491–504.
- Bouget, C., Larrieu, L., Brin, A., 2014. Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. *Ecol. Indic.* 36, 656–664.
- Bräuniger, C., Knapp, S., Kühn, I., Klotz, S., 2010. Testing taxonomic and landscape surrogates for biodiversity in an urban setting. *Landscape Urban Plann.* 97, 283–295.
- Brin, A., Brustel, H., Jactel, H., 2009. Species variables or environmental variables as indicators of forest biodiversity: a case study using saproxylic beetles in Maritime pine plantations. *Ann. For. Sci.* 66, 306–316.
- Bunnell, F.L., Huggard, D.J., 1999. Biodiversity across spatial and temporal scales: problems and opportunities. *For. Ecol. Manage.* 115, 113–126.
- Buse, J., Ranius, T., Assmann, T., 2008. An endangered longhorn beetle associated with old oaks and its possible role as an ecosystem engineer. *Conserv. Biol.* 22, 329–337.
- Cabra-García, J., Bermudez-Rivas, C., Osorio, A.M., Chacon, P., 2012. Cross-taxon congruence of alpha and beta diversity among five leaf litter arthropod groups in Colombia. *Biodivers. Conser.* 21 (6), 1493–1508.
- Caro, T., 2010. Conservation by Proxy: Indicator, Umbrella, Flagship, and Other Surrogate Species. Island Press.
- Coulon, J., Marchal, P., Pupier, R., Richoux, P., Allemand, R., Genest, L.C., Clary, J., 2000. Coléoptères De Rhône-Alpes: Carabiques Et Cicindèles. *Museum d'Histoire Naturelle de Lyon et Société Linnéenne de Lyon*, Lyon.
- Cramp, S., (coord.), 1980. The birds of the western palearctic. *Handbook of the Birds of Europe the Middle East and North Africa Vol. I-IX* Oxford University Press, New York (1994).
- Desender, K., Evynck, A., Rack, G., 1999. Beetle diversity and historical ecology of woodlands in Flanders Belgium. *J. Ecol.* 129, 139–155.
- Drapeau, P., Leduc, A., McNeil, R., 1999. Refining the use of point counts at the scale of individual points in studies of bird-Habitat relationships. *J. Avian Biol.* 30 (4), 367–382.
- Duan, M., Liu, Y., Yu, Z., Baudry, J., Li, L., Wang, C., Axmacher, J.C., 2016. Disentangling effects of abiotic factors and biotic interactions on cross-taxon congruence in species turnover patterns of plants, moths and beetles. *Sci. Rep.* 6, 23511.
- Dunn, P.K., Smyth, G.K., 1996. Randomized quantile residuals. *J. Comput. Gr. Stat.* 5, 236–244.
- Eglington, S.M., Noble, D.G., Fuller, R.J., 2012. A meta-analysis of spatial relationships in species richness across taxa: birds as indicators of wider biodiversity temperate regions. *J. Nat. Conserv.* 20 (5), 301–309.
- Ellis, D., 1985. Taxonomic sufficiency in pollution assessment. *Mar. Pollut. Bull.* 16, 459.
- FAO, 1999. *State of the World's Forests 1999*. Food and Agricultural Organisation of the United Nations, Rome.
- Failing, L., Gregory, R., 2003. Ten common mistakes in designing biodiversity indicators for forest policy. *J. Environ. Manage.* 68, 121–132.
- Fattorini, S., 2010. Biotope prioritisation in the Central Apennines (Italy): species rarity and cross-taxon congruence. *Biodiver. Conserv.* 19 (12), 3413–3429.
- Favreau, J.M., Drew, C.A., Hess, G.R., Rubino, M.J., Koch, F.H., Eschelbach, K.A., 2006. Recommendations for assessing the effectiveness of surrogate species approaches. *Biodivers. Conserv.* 15, 3949–3969.
- Fensham, R.J., Streimann, H., 1997. Broad landscape relations of the moss flora from inland dry rainforest in north Queensland, Australia. *Bryologist* 100, 56–64.
- Ford, H.A., Walters, J.R., Cooper, C.B., Debus, S.J.S., Doerr, V.A.J., 2009. Extinction debt or habitat change? Ongoing losses of woodland birds in north-eastern New South Wales, Australia. *Biol. Conserv.* 142, 3182–3190.
- Gao, T., Nielsen, A.B., Hedblom, M., 2015. Reviewing the strength of evidence of biodiversity indicators for forest ecosystems in Europe. *Ecol. Indic.* 57, 420–434.
- Gardner, T.A., Barlow, J., Araujo, I.S., Ávila-Pires, T.C., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernandez, M.I.M., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L.A.M., Miranda-Santos, R., Overal, W.L., Parry, L., Peters, S.L., Ribeiro-Junior, M.A., Da Silva, M.N.F., Motta, C., Peres, C.A., 2008. The cost-effectiveness of biodiversity surveys in tropical forests. *Ecol. Lett.* 11, 139–150. <http://dx.doi.org/10.1111/j.1461-0248.2007.01133.x>.
- Gaspar, C., Gaston, K.J., Borges, P.A., 2010. Arthropods as surrogates of diversity at different spatial scales. *Biol. Conserv.* 143, 1287–1294.
- Gaston, K.J., 1996. Biodiversity – congruence. *Prog. Phys. Geogr.* 20, 105–112.
- Gaston, K.J., 2000. Biodiversity: higher taxon richness. *Prog. Phys. Geogr.* 24, 117–127.
- Gerlach, J., Samways, M., Pryke, J., 2013. Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. *J. Insect Conserv.* 17, 831–850.
- Gosselin, F., Dallari, R., 2007. Des Suivis Taxonomiques De Biodiversité En Forêt Pourquoi? Quoi? Comment? Groupement de Nogenet sur Vernisson, CEMAGREF, pp. 1–78.
- Gosselin, F., 2011. A new calibrated bayesian internal goodness-of-Fit method: sampled posterior p-values as simple and general p-values that allow double use of the data. *PLoS One* 6, e14770.
- Grand, J., Buonaccorsi, J., Cushman, S.A., Griffin, C.R., Neel, M.C., 2004. A multiscale landscape approach to predicting bird and moth rarity hotspots, in a threatened pitch pine-scrub oak community. *Conserv. Biol.* 18, 1063–1077.
- Heink, U., Kowarik, I., 2010. What criteria should be used to select biodiversity indicators? *Biodiver. Conserv.* 19, 3769–3797.
- Herrault, P.-A., Larrieu, L., Cordier, S., Gimmi, U., Lachat, T., Quin, A., Sarthou, J.P., Sheeran, D., 2016. Combined effects of history, morphology, connectivity and structural heterogeneity of woodlands on species richness of hoverflies (Diptera: syrphidae). *Landscape Ecol.* 31, 877–893.
- Jahns, H.M., 1989. *Guide des fougères, mousses et lichens d'Europe*. Delachaux et Niestlé.
- Jonsson, B.G., Jonsell, M., 1999. Exploring potential biodiversity indicators in boreal forests. *Biodiver. Conserv.* 8, 1417–1433.
- Kati, V., Devillers, P., Dufrene, M., Legakis, A., Vokou, D., Lebrun, P., 2004. Testing the value of six taxonomic groups as biodiversity indicators at a local scale. *Conserv. Biol.* 18, 667–675.
- Kerr, J.T., 1997. Species richness, endemism, and the choice of areas for conservation. *Conserv. Biol.* 11, 1094–1100.
- Lambeck, R.J., 1997. Focal species: a multi-species umbrella for nature conservation. *Conserv. Biol.* 11 (4), 849–856.
- Landres, P.B., Verner, J., Thomas, J.W., 1988. Ecological uses of vertebrate indicator species: a critique. *Conserv. Biol.* 2, 316–328.
- Larrieu, L., Gonin, P., 2008. L'indice de Biodiversité Potentielle (IBP): une méthode simple et rapide pour évaluer la biodiversité potentielle des peuplements forestiers. *Rev. For. Fr.* 2006–2008, 727–748.
- Larsson, T.B., 2001. Biodiversity evaluation tools for European forests. *Ecol. Bull.* 50.
- Legendre, P., De Caceres, M., 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecol. Lett.* 16 (8), 951–963.
- Lindenmayer, D.B., Margules, C.R., Botkin, D.B., 2000. Indicators of biodiversity for ecologically sustainable forest management. *Conserv. Biol.* 14 (4), 941–950.
- Lombard, A.T., 1995. The problems with multi-species conservation: do hotspots, ideal reserves and existing reserves coincide? *S. Afr. J. Zool.* 30, 145–163.
- Lovell, S., Hamer, M., Slotow, R., Herbert, D., 2007. Assessment of congruency across invertebrate taxa and taxonomic levels to identify potential surrogates. *Biol. Conserv.* 139, 113–125.
- Magurran, A.E., 2004. *Measuring Biological Diversity*. Blackwell Science, Oxford, UK.
- Mandelik, Y., Roll, U., Fleischer, A., 2010. Cost-efficiency of biodiversity indicators for Mediterranean ecosystems and the effects of socio-economic factors. *J. Appl. Ecol.* 47 (6), 1179–1188.
- Mandelik, Y., Dayan, T., Chikatunov, V., Kravchenko, V., 2012. The relative performance of taxonomic vs: environmental indicators for local biodiversity assessment: a comparative study. *Ecol. Indic.* 15 (1), 171–180.

- Millar, R.B., 2009. Comparison of hierarchical bayesian models for overdispersed count data using DIC and bayes' factors. *Biometrics* 65 (3), 962–969.
- Mills, L.S., Soule, M.E., Doak, D.F., 1993. The keystone-Species concept in ecology and conservation. *Bioscience* 43 (4), 219–224.
- Moran, M.D., 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* 100, 403–405.
- Murdoch, W.W., Evans, F.C., Peterson, C.H., 1972. Diversity and pattern in plants and insects. *Ecology* 53, 819–829.
- Mysak, J., Horsak, M., 2014. Biodiversity surrogate effectiveness in two habitat types of contrasting gradient complexity. *Biodiver. Conserv.* 23 (5), 1133–1156.
- Nageleisen, L.M., Bouget, C., coord, 2009. *Forest Insect Studies: Methods and Techniques. Key Considerations for Standardization. An Overview of the Reflections of the Entomological Forest Inventories Working Group. Les Dossiers Forestiers n°10.* ONF.
- Negi, H.R., Gadgil, M., 2002. Cross-taxon surrogacy of biodiversity in the Indian Garhwal Himalaya. *Biol. Conserv.* 105, 143–155.
- Nordén, B., Paltto, H., Götmark, F., Wallin, K., 2007. Indicators of biodiversity, what do they indicate? Lessons for conservation of cryptogams in oak-rich forest. *Biol. Conserv.* 135, 369–379.
- Noss, R.F., 1990. Indicators for monitoring biodiversity – a hierarchical approach. *Conserv. Biol.* 4, 355–364.
- Oliver, I., Beattie, A.J., 1996. Designing a cost-effective invertebrate survey: a test of methods for rapid assessment of biodiversity. *Ecol. Appl.* 6, 594–607.
- Ovaskainen, O., Schigel, D., Ali-Kovero, H., Auvinen, P., Paulin, L., Nordén, B., Nordén, J., 2013. Combining high-throughput sequencing with fruit body surveys reveals contrasting life-history strategies in fungi. *ISME J.* 7, 1696–1709.
- Peres-Neto, P., Jackson, D., 2001. How well do multivariate data sets match? The advantages of a Procrustean superimposition approach over the Mantel test. *Oecologia* 129, 169–178.
- Pharo, E.J., Beattie, A.J., Binns, D., 1999. Vascular plant diversity as a surrogate for bryophyte and lichen diversity. *Conserv. Biol.* 13, 282–292.
- Pierson, J.C., Barton, P.S., Lane, P.W., Lindenmayer, D.B., 2015. Can habitat surrogates predict the response of target species to landscape change? *Biol. Conserv.* 184, 1–10.
- Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C., Gibbons, D.W., 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* 365, 335–337.
- Prendergast, J.R., 1997. Species richness covariance in higher taxa: empirical tests of the biodiversity indicator concept. *Ecography* 20, 210–216.
- Puimalainen, J., Kennedy, P., Folving, S., 2003. Monitoring forest biodiversity: a European perspective with reference to temperate and boreal forest zone. *J. Environ. Manage.* 67 (1), 5–14.
- R Development Core Team, 2013. *R: a Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna.
- Rameau, J.C., Mansion, D., Dumé, G., 1989. *Flore Forestière Française. Tome 1: Plaines Et Collines.* IDF, Paris.
- Rameau, J.C., Mansion, D., Dumé, G., 1993. *Flore Forestière Française. Tome 2: Montagnes.* IDF, Paris.
- Ranius, T., 2002. Osmoderma eremita as an indicator of species richness of beetles in tree hollows. *Biodiver. Conserv.* 11, 931–941.
- Rice, W.R., 1989. Analyzing tables of statistical tests. *Evolution* 43, 223–225.
- Ricketts, T.H., Daily, G.C., Ehrlich, P.R., 2002. Does butterfly diversity predict moth diversity? Testing a popular indicator taxon at local scales. *Biol. Conserv.* 103, 361–370.
- Rooney, R.C., Azaria, E.T., 2015. The strength of cross-taxon congruence in species composition varies with the size of regional species pools and the intensity of human disturbance. *J. Biogeogr.* 42 (3), 439–451.
- Runnel, K., Tamm, H., Lõhmus, A., 2015. Surveying wood-inhabiting fungi: most molecularly detected polypore species form fruit-bodies within short distances. *Fungal Ecol.* 18, 93–99. <http://dx.doi.org/10.1016/j.funeco.2015.08.008>.
- Sabatini, F.M., Burrascano, S., Azzella, M.M., Barbati, A., De Paulis, S., Di Santo, D., Facioni, L., Giuliarrelli, D., Lombardi, F., Maggi, O., Mattioli, W., Parisi, F., Persiani, A., Ravera, S., Blasi, C., 2016. One taxon does not fit all: herb-layer diversity and stand structural complexity are weak predictors of biodiversity in *Fagus sylvatica* forests. *Ecol. Indic.* 69, 126–137.
- Saetersdal, M., Gjerde, L., Blom, H.H., Ihlen, P.G., Myrseth, E.W., Pommeresche, R., Skartveit, J., Solhoy, T., Aas, O., 2003. Vascular plants as a surrogate species group in complementary site selection for bryophytes, macrolichens, spiders, carabids, staphylinids, snails, and wood living polypore fungi in a northern forest. *Biol. Conserv.* 115, 21–31.
- Santi, E., Maccherini, S., Rocchini, D., Bonini, I., Brunialti, G., Favilli, L., Perini, C., Pezzo, F., Piazzini, S., Rota, E., Salerni, E., Chiarucci, A., 2010. Simple to sample: vascular plants as surrogate group in a nature reserve. *J. Nat. Conserv.* 18 (1), 2–11.
- Santi, E., Bacaro, G., Rocchini, D., Chiarucci, A., Bonini, I., Brunialti, G., Muggia, L., Maccherini, S., 2016. Methodological issues in exploring cross-taxon congruence across vascular plants, bryophytes and lichens. *Folia Geobotanica* 51 (4), 297–304.
- Sauberer, N., Zulka, K.P., Abensperg-Traun, M., Berg, H.M., Bieringer, G., Milasowsky, N., Moser, D., Plutzer, C., Pollheimer, M., Storch, C., Trostl, R., Zechmeister, H., Grabherr, G., 2004. Surrogate taxa for biodiversity in agricultural landscapes of eastern Austria. *Biol. Conserv.* 117, 181–190.
- Sebek, P., Barnounin, T., Brin, A., Brustel, H., Dufrène, M., Gosselin, F., Meriguet, B., Micas, L., Noblecourt, T., Rose, O., Velle, L., Bouget, C., 2012. A test for assessment of saproxylic beetle biodiversity using subsets of monitoring species. *Ecol. Indic.* 20, 304–315.
- Simberloff, D., 1998. Flagships, umbrellas, and keystones: is single-species management passe in the landscape era? *Biol. Conserv.* 83, 247–257.
- Similä, M., Kouki, J., Monkkonen, M., Sippola, A.L., Huhta, E., 2006. Co-variation and indicators, of species diversity: can richness of forest-dwelling species be predicted in northern boreal forests? *Ecol. Indic.* 6, 686–700.
- Sommaggio, D., Burgio, G., 2003. Role of Diptera Syrphidae as landscape indicators: analysis of some case studies in Northern Italy. *Bull. Oib/Srop.* 26, 145–150.
- Speight, M.C.D., Castella, E., Sarthou, J.P., 2013. Speight. In: Speight, M.C.D., Castella, E., Sarthou, J.-P., Vanappelghem, C. (Eds.), *Syrph the Net on CD, Issue 9. The Database of European Syrphidae.* Syrph the Net Publications, Dublin.
- Vellend, M., Lilley, P.L., Starzomski, B.M., 2008. Using subsets of species in biodiversity surveys. *J. Appl. Ecol.* 45, 161–169.
- Westgate, M.J., Barton, P.S., Lane, P.W., Lindenmayer, D.B., 2014. Global meta-analysis reveals low consistency of biodiversity congruence relationships. *Nat. Commun.* 5.
- Westgate, M.J., Tulloch, A.I.T., Barton, P.S., Pierson, J.C., Lindenmayer, D.B., 2017. Optimal taxonomic groups for biodiversity assessment: a meta-analytic approach. *Ecography* 40 (4), 539–548.
- Williams, P.H., Gaston, K.J., 1994. Measuring more of biodiversity – can higher-Taxon richness predict wholesale species richness. *Biol. Conserv.* 67, 211–217.
- Wolters, V., Bengtsson, J., Zaitsev, A.S., 2006. Relationship among the species richness of different taxa. *Ecology* 87, 1886–1895.
- Yu, D.W., Ji, Y., Emerson, B.C., Wang, X., Ye, C., Yang, C., Ding, Z., 2012. Biodiversity soup: metabarcoding of arthropods for rapid biodiversity assessment and biomonitoring. *Methods Ecol. Evol.* 3, 613–623.