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To what extent can management variables explain species assemblages? A study of carabid beetles in forests

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Studies concerning the influence of forest management on invertebrate communities often focus on a limited set of chosen variables and rarely quantify the importance of management as opposed to other influences. We aimed at: 1) comparing the importance for species assemblages of habitat variables defined by management with those independent of it; 2) understanding the ecological significance of the variation remaining when both management and non-management variables are used. We caught carabid beetles according to a stratified pitfall sampling based on forest structure, tree composition and stand age. Forty-nine habitat variables were measured using three spatial scales. We decomposed the variation of species assemblages with successive constrained ordinations based on sets of variables, and studied the life traits of the species least and best explained by the model including all of the variables. Forest structure, composition and stand age showed important effects but explained a relatively small part of the overall variation in species assemblages. Management accounted for ca 30% of the variation, but non-management variables had a significant impact and the interaction between management and non-management sets resulted in significant influences. Most species for which the variation was highly explained by the model were generally large and with inefficient wings, while the least explained species were small. Our study suggests that: 1) even with highly controlled samples, the influence of management on species assemblages should not be studied by a limited set of categorical variables; 2) management variables may interact with factors outside of the manager's control; 3) a significant part of the variation cannot be explained by habitat variables and needs taking ecological processes into account; 4) rules to optimise constrained ordination techniques applied to species-habitat studies can be proposed.

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Quantifying the impact of management on forest invertebrate assemblages and identifying the key variables is an important issue for ecologists and foresters (Eyre and Rushton 1989, Ferris and Humphrey 1999). Forest management is supposed to be a major source of change in forest biodiversity (Hunter 1999), particularly for invertebrates (Speight 1989). In forests, factors such as stand structure, composition and age have been shown to significantly influence invertebrate assemblages (Baguette and Gérard 1993, Irmler et al. 1996, Humphrey et al. 1999). However, the relative importance of all possible explanatory variables is poorly known. Most

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management impact studies focus on the apparent effect of chosen habitat gradients or on differences between selected habitat types, without questioning the meaning of the variation unexplained (Baguette and Gérard 1993, Buse and Good 1993, Schowalter 1995, Jukes et al. 2001). In such cases, the effect of management may be mixed with other habitat influences and a relatively large part of the species-sites relationship may be simply ignored. How can we overcome this problem?

In this paper, we aim 1) to compare the importance for species assemblages of habitat variables defined by management with those independent of it, and 2) to understand the ecological significance of the variation remaining when both management and non-management variables are taken into account. We use a progressive decomposition of the variation in species assemblages with ordinations constrained by chosen sets of variables: we start with three variables classically used to assess forest management impact (stand structure, composition and age), add other variables directly defined by felling and regeneration operations and, finally, include a set of habitat features not directly and solely defined by management practices. We then try to understand the residual variation by studying the link between life traits and the variation explained at the species level. By attempting to answer the questions mentioned above, we also study how to optimise regression models relating species assemblages to habitat variables.

We used carabid beetles (Coleoptera) as indicators of forest invertebrate fauna. This group is well documented, is known to be very sensitive to changes in habitat conditions (Baguette 1993) and includes a diversity of life history traits (size, mobility, habitat preferences, etc.).

Materials and methods

Study area

Willing to study management's impact on carabid assemblages, we chose a region relatively homogeneous in terms of soil, climate and landscape features. The Ardennes is mostly composed of pastures and woodlands, partially transformed into commercial conifer stands in the last 150 yr (Devillez and Delhaise 1991). It is characterised by a humid sub-mountainous climate, soft hilly relief and loamy acid soils. In the sampling zones, the altitude ranges from 320 to 560 m, mean annual rainfall from 1050 to 1200 mm yr^{-1} and mean annual temperatures from 6.9 to 7.8°C (Weissen et al. 1994). All the study plots were set up on Luzulo-Fagetum or Luzulo-Quercetum potential vegetation according to the classifications of Noirfalise (1984) and Rameau et al. (2000), on flat or very slightly sloping ground of acid brown and moderately dry soils (Dystric cambisol: Anon. 1990). The plot soils were very similar in terms of water and nutrient availability (Table 1). We kept a minimum distance of 100 m between any two plots and 100 m from the nearest agricultural habitat (crop or meadow). The tree species in the forests being studied were mostly spruce *Picea abies*, Douglas fir *Pseudotsuga menzienzii*, beech *Fagus sylvatica* and oak *Quercus petraea* and *Quercus robur.*

Data on carabid beetles

Three pitfalls were placed in an equilateral triangle of 3 m per side in each plot, and emptied monthly from 10 April to 5 November. The pitfalls were cylindrical, 8.5 cm large and 17 cm deep (Dufrêne 1988); formaldehyde 5% was used as killing and conserving agent. Pitfall traps provide valuable information on the activity and relative abundance of carabid species, but relatively poor data on their absolute abundance and density as Kinnunen et al. (2001) suggested. They are useful for comparative studies such as the one presented in this paper. Identification of carabids was principally carried out with the help of Lindroth (1974), according to the nomenclature of the Belgian Royal Society of Entomology (Coulon 1995).

Overall, 69 species were found; however, we retained only the 51 species appearing in more than two plots in the data set. The abundance of each species is given in the Appendix. A log-transformation was applied to abundance before each ordination analysis (see Data analysis).

Environmental variables

Sampling scheme

As described in du Bus de Warnaffe and Lebrun (2004), the plots were chosen according to three variables: stand structure and stand composition at the 15-ha scale, and mean age of the trees at the local scale (0.04 ha). Stand structure designs the size of the patches in the forest, in three classes (>2, 0.2–0.5, <0.2 ha), and stand composition the major tree species composing the canopy, in four classes (beech, oak, spruce-Douglas fir, beech-spruce-Douglas fir). Both are valuable descriptors of forest management systems in tall forests (Kerr 1999), and seem to be key factors in the distribution of carabid species in forests (Butterfield et al. 1995, Ings and Hartley 1999, Jukes et al. 2001). They were determined by GIS, after mapping the stands of similar age and composition on aerial photographs. In each class defined by stand structure and composition, we chose two plots for each of three age classes: age 1 or "regeneration" (trees 3–10 yr old), age 2 or "medium-aged stands" (20–40 yr old for conifer stands, 30–60 yr old for broadleaf stands), and age 3 or "mature stands" (stage 3:

Table 1. Number of plots by sampling class, and main features of each class. All plots were situated on flat or very little sloping ground, on acid brown and moderately dry soils (Dystric cambisol: Anon. 1990). Soil water availability class was measured according to the classification of Weissen et al. (1994), an alphabetic scale ranging from a (very dry) to i (very moist). Mean dbh (diameter at breast height) and basal area were measured at 0.20 ha scale.

Stand structure (15 ha)		Even-aged			Group Mixed	Uneven-aged		
Stand composition (15 ha)		Conifer	Beech	Oak		Conifer	Beech	Total
Number of plots: (age: 0.04 ha)	young (1)	8	6	6	6	5	10	41
	medium-aged (2)	8	6	6	6	7	10	43
	mature (3)	8	6	8	6	6	10	44
Total number of plots		24	18	20	8	18	30	128
Altitude (m)	1	380–520	410–540	320–390	390–560	420–580	410–500	–
	2	320–490	380–540	320–400	390–560	420–580	350–500	–
	3	320–520	380–460	320–390	390–560	420–580	350–500	–
Upper soil pH_{H_2O} (5 cm)	1	4.1–4.7	4.1–4.5	4.2–4.5	3.8–4.2	3.8–4.2	4.0–4.3	–
	2	4.2–4.4	3.8–4.4	4.3–4.6	3.8–4.2	3.6–4.2	3.8–4.3	–
	3	3.8–4.1	3.8–4.3	4.2–4.8	3.8–4.2	3.8–4.2	3.8–4.2	–
Soil water availability	1	b	b (c)	b (c)	b (c)	b (c)	b	–
	2	b	b	b–c	b	b	b	–
	3	b	b	b (c)	b	b	b	–
Mean dbh on 0.20 ha (cm)	1	2–7	2–6	2–9	1–6	2–8	1–8	–
	2	20–27	28–44	32–38	20–37	22–36		–
	3	43–50	43–59	39–44	27–50	41–52	34–52	–
Basal area (m^2 ha^{-1})	1	1–7	1–5	2–12	6–14	18–27	11–20	–
	2	34–41	21–31	20–24	21–44	32–40	17–28	–
	3	47–53	22–28	19–25	23–44	31–42	21–29	–
Size of the stand (ha)	1	4–12	3–6	2–5	0.15–0.40	0.02–0.15	0.03–0.20	–

50–80 yr old for conifer, 80–140 yr old for broadleaf). Age was determined on the field. We will refer to these variables as "structure", "composition" and "age"; together they define what will be called the "sampling structure" (SS). Five to ten plots were selected for each structure/composition/age class. In all, 128 plots were selected (Table 1).

Uncontrolled variables

Twelve variables related to management practices were measured using three spatial scales: 0.04, 0.20 and 3 ha (Table 2, columns 1 and 2). The first two scales were treated by field measurements, the third by GIS on aerial photographs. Several variables were not measurable on certain stand age(s), as shown in Table 2. Stand size for medium-aged and mature stands was measured but eliminated since it had no significant relationship to species assemblages (see Analysis scheme).

In order to remove the redundant variables for reducing noisy effects (MacCune 1997), we performed a correlation analysis and suppressed the variables on 0.20 and/or 3 ha when the same variable on 0.04 ha explained >50% of their variance ($r^2 > 0.50$; $p < 0.0001$). We applied this scheme separately to young stands and to medium-aged+mature stands because the sets of available explanatory variables were different (see Table 2). In fact, none of the 0.20 ha scale variables were useful except "vertical-" and "horizontal canopy heterogeneity", but all 3-ha variables had to be kept. Within each spatial scale, no variables were redundant, except % medium-aged with % young and % mature at the 3-ha scale (we dropped % medium-aged). In all, 24 variables were retained.

We measured 13 variables not controlled by forest managers at the 0.04 ha scale (Table 2). The Lambert spatial coordinates and their square order combinations (x, y, xy, x^2, y^2) were used to evaluate the significance of spatial auto-correlation (Borcard et al. 1992). Hence, three sets of uncontrolled explanatory variables were built as given in Table 2: forest management variables (FM), non-management variables (NM), and spatial coordinates (XY).

Data analysis

Conceptual background

We used linear ordination techniques with Canoco 4.0 (ter Braak and Smilauer 1998). Indirect gradient analyses such as Principal Component Analysis or Correspondence Analysis are generally applied to describe, the structure of an independent variable set or of a biological data set (Legendre and Legendre 1998). But when the objective is to quantify and describe the relationship of a particular set of variables with species assemblages, direct gradient analysis is more adapted (Økland 1996). Direct gradient analysis (ter Braak and Prentice 1988), and especially Canonical Correspondence Analysis (ter Braak 1986), makes it possible to measure the significance of different explanatory variables and sets of

Table 2. Variables used for the Canonical Correspondence Analyses. % explic = % of the variation of species profiles (CA) explained by the variable; p = value of the error probability for the Monte-Carlo randomisation test. All observations on the vegetation under the canopy (0–8m) were performed on 400 m^2, by quantifying the % cover of each present species on the Braun-Blanquet scale in four vertical vegetation layers. S34-004 was considered as management-dependent in young stands because forest technicians often cut the shrubs around the productive trees (planted or natural) in order to give them optimal growing conditions.

		Medium-a. + mature		Young	
Codes	Variables	% expl.	p-value	% expl.	p-value
Sampling structure (SS)[a]					
Age	Age class on 0.04 ha (age of most trees present)	1.72	0.021	–	–
Beech	Beech dominant (1) or not (0) on 0.04 ha	2.85	<0.001	2.20	0.032
Oak	Oak dominant (1) or not (0) on 0.04 ha	2.79	<0.001	1.92	0.047
Struc	Structure of the forest at 3 ha scale	2.35	0.003	3.64	0.002
Forest Management variables (FM)[a]					
Be-004	Percentage of beech (surface) on 0.04 ha	2.46	<0.001	1.62	>0.05
Br-004	Percentage of the litter covered by branches on 0.04 ha	1.75	0.001	1.18	>0.05
CC-004	Total canopy cover on 0.04 ha (dbh > 10 cm, m^2 ha^{-1})	<1.00	>0.05	–	–
LWD-004	Volume of large woody debris (diam > 30 cm) on 0.04 ha	<1.00	>0.05	1.41	>0.05
mD-004	Mean diameter of the trees at breast height on 0.04 ha	1.62	0.006	–	–
NSt-004	Number of stumps (diam > 10 cm) on 0.04 ha	1.36	0.042	1.88	>0.05
NTS-004	Number of tree species (dbh > 10 cm) on 0.04 ha	1.32	>0.05	–	–
O-004	Percentage of oak (surface) on 0.04 ha	2.20	<0.001	1.82	>0.05
S34-004	Total cover of the shrub layer (0.5–8 m) on 0.04 ha	–	–	2.76	0.014
SWD-004	Volume of small woody debris (d = 10–30 cm) on 0.04 ha	2.20	0.002	2.41	>0.05
VCH-004	Vertical heterogeneity of the canopy on 0.04 ha	1.17	>0.05	–	–
HCH-020	Horizontal heterogeneity of the canopy on 0.20 ha	<1.00	>0.05	–	–
VCH-020	Vertical heterogeneity of the canopy on 0.20 ha	1.29	0.048	–	–
A-3	Percentage of young stands (< 10 yr) on 3 ha	1.04	>0.05	3.18	0.004
C-3	Percentage of mature stands on 3 ha	1.81	0.003	3.24	0.004
MS-3	Mean size of the eco-units (Oldeman 1990) on 3 ha	1.36	0.031	2.76	0.011
B-3	Percentage of beech (surface) on 3 ha	2.72	<0.001	2.42	0.021
O-3	Percentage of oak (surface) on 3 ha	2.07	<0.001	2.40	>0.05
SYS	Size of the young stand (ha)	–	–	3.24	0.002
Non-management variables (NM)[b]					
Alt	Mean altitude of the plot (flat fields in most cases)	1.20	0.030	3.25	0.001
Dagr	Distance to the nearest agricultural habitat (meadow, crop)	<1.00	>0.05	1.69	0.042
Ddec-004	Mean decomposition degree of the woody debris on 0.04 ha	<1.00	>0.05	1.17	>0.05
HL-004	Hydric level of the soil (Weissen et al. 1994)	<1.00	>0.05	1.48	>0.05
Mos-004	Cover of mosses on the low bark of large trees on 0.04 ha	1.07	>0.05	–	–
pH-004	Mean pH-H_2O of the soil (0–10 cm) on 0.04 ha	<1.00	>0.05	<1.00	>0.05
Rh-004	Species richness of the shrub layer (0.5–8 m) on 0.04 ha	1.09	0.031	1.10	>0.05
Rsh-004	Species richness of the herbaceous layer (0.5–8 m) on 0.04 ha	<1.00	>0.05	1.23	>0.05
S1mos-004	Cover of mosses in the vegetation layer 0–0.12 m on 0.04 ha	1.12	0.020	1.11	>0.05
S1vp-004	Cover of vascular plants in the layer 0–0.12 m on 0.04 ha	<1.00	>0.05	2.67	0.002
S2-004	Total cover of the vegetation layer 0.12–0.5 m on 0.04 ha	<1.00	>0.05	4.08	<0.001
S34-004	Total cover of the shrub layer (0.5–8 m) on 0.04 ha	1.09	0.048	–	–
SL-004	Slope of the plot (degrees)	<1.00	>0.05	<1.00	>0.05
Spatial co-ordinates (XY)[b]					
x	Lambert x co-ordinate	1.42	0.027	2.06	0.031
x^2	Square of the Lambert x co-ordinate	1.41	0.021	1.94	0.041

[a] values computed after removing the effects of NM and XY variable sets (Table 3, step 2);
[b] values computed after removing the effects of SS and FM variable sets (Table 3, step 2).

variables (Borcard et al. 1992) and ecologists have already used it for this purpose (Økland and Odd 1994, Anderson and Gribble 1998, Cushman and MacGarigal 2002, Cushman and Wallin 2002). However, partialling out the variation of species assemblages was rarely used for studying management impact, although it seems to offer some very interesting insights, at least when precise hypotheses have to be tested (Økland 1999).

We performed Redundancy Analyses (RDA) for linear relations and Canonical Correspondence Analyses (CCA) for non-linear relationships (ter Braak 1986, ter Braak and Smilauer 1998). CCA has the advantage of being less influenced by noise in species abundance and by intercorrelated environmental variables than other methods (Gauch 1982, Palmer 1993). It allows calculating the proportion of variation of a biological data set explained by a set of independent variables (environment file), eventually taking the effect of another set of independent variables into account (covariable file) (Borcard et al. 1992).

When two matrixes **A** (biological data) and **B** (environment file) are compared, the variation of A (written as A) can be broken down according to the equation:

$$A = B + A|B \qquad (1)$$

where B is the variation explained by B and A|B the variation not explained by B.

Dividing B into B_1 and B_2, the variation of A can be broken down as:

$$A = B_1|B_2 + B_2|B_1 + (B_1 \cap B_2) + A|(B_1 \cup B_2) \qquad (2)$$

where $B_1|B_2$ is the variation explained by B_1 independently from B_2, $B_2|B_1$ the variation explained by B_2 independently from B_1, $(B_1 \cap B_2)$ the variation explained by the interaction between B_1 and B_2 (shared by both) and $A|(B_1 \cup B_2)$ the variation not explained by B_1 and B_2.

Since $(B_1 \cap B_2) = B_1 - B_1|B_2$, a first CCA with B_1 as the environment file and B_2 as the covariable file gives $B_1|B_2$ and $(B_1 \cap B_2)$. A second CCA with B_2 as the environment file and B_1 as the covariable file gives $B_2|B_1$. These analyses are called "partial CCA" (ter Braak 1988, Cushman and Wallin 2002). Using eq. 2, a simple deduction provides the remaining component, $A|(B_1 \cup B_2)$. This series of CCA constitutes a method called "CCA with variation partitioning" (Økland and Odd 1994).

Analysis scheme

First of all, the general structure of the carabid file was illustrated by Correspondence Analysis (CA) (Hill 1974), providing an initial "neutral" view of species-sites relationships, which is complementary to any direct gradient analysis (Økland 1996). We then studied the relationship between controlled and uncontrolled variables, in order to quantify the level of inter-dependence between variable sets. The relationships between SS, FM, NM and XY were computed with RDA on the basis of eq. 1.

Finally, we applied CCA with variation partitioning. The variables associated with the sampling structure were first transformed from categorical to ordinal ones (ter Braak 1986), according to the following system: for the structure: U = 1, G = 2, E = 3; for the composition: O = 1 and B = 0 for oak, O = 0 and B = 1 for beech and O = 0, B = 0 for conifer; for the age: young = 1; medium-aged = 2; mature = 3. We did not use any computerised method of variable selection (e.g. stepwise selection with SAS), since this often creates unstable models, especially with inter-correlated variables. Instead, we separately studied each variable by the Monte-Carlo randomisation test with 999 steps in an initial CCA with all variables (eq. 1) and dropped the ones that proved to be non-active ($p > 0.05$); this allowed us to reduce the possible proportion of variation due to random effects (MacCune 1997). The resulting list of variables is given in Table 2.

To reach our goals, three analysis steps based on CCA were necessary (Table 3). In a first step, we quantified the variation in species assemblages explained by SS, without any covariable and with all variables not related to forest management (NM and XY) as the covariable file, using eq. 2. In a second step, we quantified the

Table 3. (a) Sets of explanatory variables used with CCA to perform the analysis steps 1 to 3 (Section 2.4.2). (b) Results: % explained. The numbers of variables in the files are given in brackets.

Step	Question	Equation	Explanatory variables sets	
(a)				
1	Effect of SS independently of the uncontrolled variables (NM and XY)	(2)	$B_1 = SS$	$B_2 = NM \cup XY$
2	Forest management vs other variables	(2)	$B_1 = SS \cup FM$	$B_2 = NM \cup XY$
3	Variability explained by all* variables	(1)	$B = SS \cup FM \cup NM \cup XY$	–

Step	Age	Variable set B_1 (or B)	Set B_2	$A\|B_1$	$A\|B_2$	B_1	B_2	$B_1\|B_2$	$B_2\|B_1$	$B_1 \cap B_2$	Unexp.
(b)											
1	1	SS (3)	$NM \cup XY$ (13)	78	36	22	64	8	49	14	29
	2+3	SS (4)	$NM \cup XY$ (15)	85	72	15	28	10	19	6	65
2	1	$SS \cup FM$ (16)	$NM \cup XY$ (13)	37	44	63	56	30	22	33	15
	2+3	$SS \cup FM$ (21)	$NM \cup XY$ (15)	62	72	38	28	29	16	9	45
3	1	$SS \cup FM \cup NM \cup XY$ (29)	–	–	–	85	–	–	–	–	15
	2+3	$SS \cup FM \cup NM \cup XY$ (36)	–	–	–	55	–	–	–	–	45

A = carabid species/sites file.
SS = sampling structure; NM = variables not related to forest management; XY = spatial coordinates (x, y, xy, x^2, y^2); FM = variables related to forest management but not included in SS (non-controlled).
* = only significantly acting ($p < 0.05$), not redundant and biologically founded variables (see text).
Unexp. = variability unexplained by the used variable set(s).

relative part of variation explained by all variables linked to forest management (SS and FM), and of all other variables (NM and XY), using eq. 2. We thereby identified the most important explanatory variables and the relationships between species and these variables. In a third step, we quantified the variation explained by all measured variables using eq. 1. The possibility of a remaining structure in the residual variation related to unconsidered variables was then visually tested, using the position of plots on the first axes of the CCA performed with all variables as the covariable file. To analyse the ecological meaning of the residual variation, we identified the life traits of species the least and the best explained by all used variables.

Results

Preliminary analyses

Carabid data structure
The first axis of the CA performed on all plots showed that carabid communities strongly react to the distinction between young and older stands (Fig. 1). Young stands (age 1) were principally characterised by the presence of *B. harpalinus*, *P. cupreus*, *D. globosus*, *P. versicolor*, *A. communis*, *A. lunicollis*, *A. binotatus*, *B. lampros*, *P. strenuus*, *T. secalis*, *T. nitens*, *H. quadripunctatus* and *H. latus* while stands of age 2 and 3 were only characterised by the presence of *A. assimile* and *N. biguttatus*. Strong differences in relative abundance were identified (Appendix). Hence, for all further analyses, we divided all files into two parts: young stands (age 1, 41 plots, 44 species) and medium-aged + mature stands (age 2 + 3, 87 plots, 35 species).

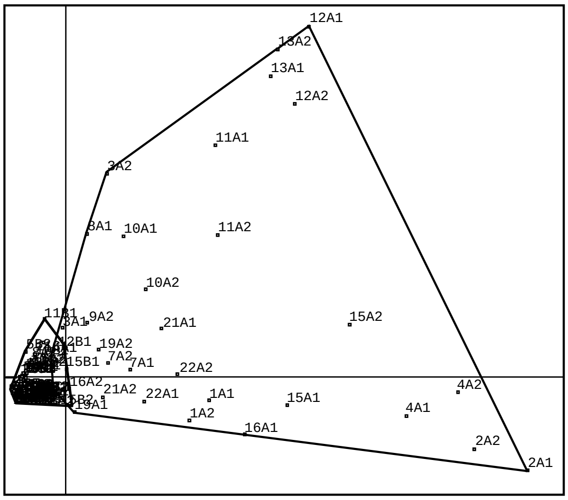


Fig. 1. Initial Correspondance Analysis on all plots (128 plots, 51 species). Broken lines design all the plots of age 1 and continue lines the plots of ages 2 and 3.

Relationships between explanatory variables
The RDA revealed a strong link between sampling structure (SS) and forest management variables (FM) for both young and older stands (Fig. 2). However, FM included information not contained in SS (45% in young stands and 21% in medium-aged and mature stands). SS and FM were linked with non-management (NM) and spatial variables (XY), though the sampling was constructed to avoid this relationship. However, SS only explained a small part of NM and XY, suggesting that these sets of variables describe aspects of the sites not considered by the sampling structure. NM and XY data sets were also linked, at least in ages 2 and 3.

Variation explained by management

The sampling structure explained 22% of the variation in species assemblages in young stands, and 15% in medium-aged and mature stands; but when the effect of NM and XY was removed (partial CCA), SS only explained 8 and 10%, respectively (Table 3). A significant part of the apparent effect of SS was due to an interaction with NM and XY (14 and 5%). Conversely, when the effect of SS was removed, NM and XY together explained 49% of variation in species assemblages in young stands, and 19% in medium-aged and mature stands.

When the effects of NM and XY were removed, all variables related to management ($SS \cup FM$) explained 30% of the variation in species assemblages in young stands and 29% in older stands (Table 3 and Fig. 3). Hence, the addition of uncontrolled significant variables related to management clearly improved the explicative power of forest management. However, 37–62% variation was independent of the variables used to describe forest management (Fig. 3).

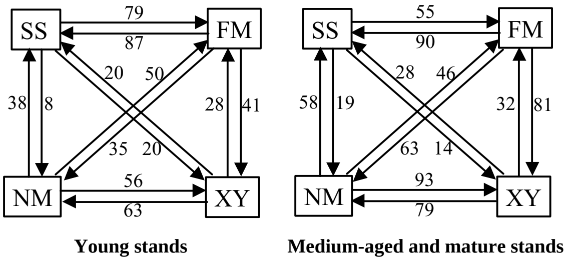


Fig. 2. Relationships between sets of explicative variables in young stands (stage 1) and in older stands (stages 2 and 3) as a result of the Redundancy Analysis (RDA). Each arrow gives the part of variation (%) of one set explained by another set. SS = sampling structure; FM = management variables; NM = non-management variables; XY = spatial coordinates. For instance, in young stands SS explains 79% of FM, and FM explains 87% of SS.

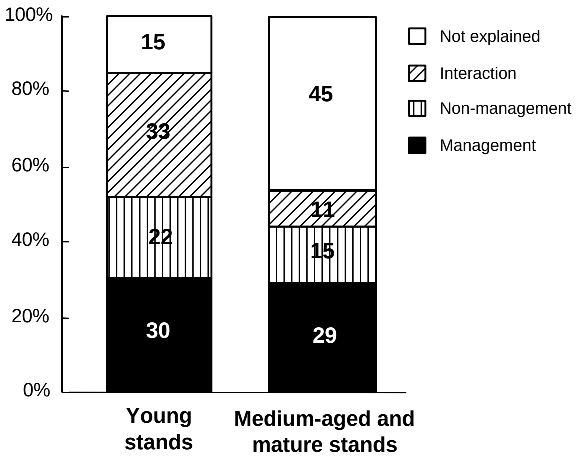


Fig. 3. Part of variation of species assemblages (CA) explained by management variables, other variables, and the interaction between both groups (CCA), in young stands and in medium-aged and mature stands.

The first two axes of the CCA for young stands accounted for 32% of the species-variable relationships and 10% of the carabid data. The most important variables were the size of the stand (correlated with Struc and A-3), the proportion of young and of mature stands on 3 ha, and the cover of the shrub layer (Fig. 4a). Management variables explained >40% of the variation for ten species (*L. pilicornis*, *P. rhaeticus*, *A. ovata*, *P. angustatus*, *A. ater*, *P. cristatus*, *C. nemoralis*, *A. binotatus*, *N. palustris*, *C. monilis*). *Notiophilus palustris*, *P. cristatus*, *A. binotatus*, *B. harpalinus* and *B. mannerheimi* appeared to be associated with large young stands in beech forests (Fig. 4a, left), while *P. angustatus*, *C. campestris* and *D. globosus* favoured large young stands in oak or conifer forests (Fig. 4a, down). *Leistus piceus, A. ovalis, C. attenuatus* and *T. laevicollis* is obviously associated with gaps in uneven-aged beech forests (Fig. 4a, up). *Loricera pilicornis*, *C. nemoralis* and *A. ovata* seemed to be associated with gaps in uneven-aged conifer forests, characterised by a well-developed shrub layer (high S34-004) (Fig. 4a, right). *Carabus monilis*, *P. madidus* and *C. problematicus* seemed to be associated with small young stands with a well-developed shrub layer.

The two first axes of the CCA for medium-aged and mature stands accounted for 34% of the species-variable relationships and 10% of the carabid data. The important forest management variables were tree species composition (beech, oak or conifer, bottom right), ground cover (stumps, woody debris and branches), percentage of mature stands on 3 ha, and mean diameter of the trees (Fig. 4b). Management variables explained >40% of the variation for four species (*A. assimile*, *C. problematicus*, *C. inquisitor*, *C. auronitens*) and 30–40% of the variation for six species (*P. niger*, *P. oblongopunctatus*, *T. laevicollis*, *A. lunicollis*, *B. lampros*, *L. pilicornis*). *A. lunicollis*, *A. muelleri*, *C. inquisitor*, *A. parallelus* and *C. arvensis* appeared to be clearly associated with oak stands. *Abax ovalis*, *T. obtusus, P. cristatus* and *C. attenuatus* is associated with beech stands. *Agonum assimile*, *N. biguttatus* and *D. globosus* seemed to be associated with conifer stands characterised by a high density of stumps and the cover of litter by branches and small woody debris.

Variation explained by all variables, and link with species life traits

When taken together, the sampling structure and all uncontrolled variables explained 85% of the variation in the carabid data in young stands and 55% in medium-aged and mature stands (Table 3). The CCA performed with all variables as the covariable file provided Axes 1–2 and Axes 3–4 plans where we did not find any structure in the arrangement of plots that we could relate to possible unmeasured variables. Hence, 15–45% of the variation of local carabid assemblages could not be explained by habitat variables with this spatially and temporally focused sampling and variable measurement.

Species best and least explained by all variables are given in Table 4. In medium-aged and mature stands, little-explained species had low abundance except *N. brevicollis* and *T. secalis*, while all of the best-explained species were abundant except *A. assimile* (see Appendix). In young stands, this was not obvious. Moreover, in both habitat types, the most abundant species were not the best explained. Thus, there was no clear relationship between explained variation and abundance, which indicates that the unexplained variation cannot only be due to rare species. In medium-aged and mature stands, the best explained species were all typical forest dwellers except *C. violaceus* (also frequent on peat bogs: Desender et al. 1995) and large species with inefficient wings except *A. assimile* (Table 4). However, the three most abundant species (*A. ater, C. problematicus, P. oblongopunctatus*) were relatively poorly explained, although they were also large forest species with inefficient wings. In young stands, the best explained species were large species with inefficient wings, except *P. angustatus* (macropterous) and *N. palustris* (small). The least explained were generally small but no clear trend appeared concerning their mobility for young as well as for older stands.

Discussion

The risk of relating variation to sampling variables only

Sampling variables explained relatively small parts of variation in species assemblages, though our sampling

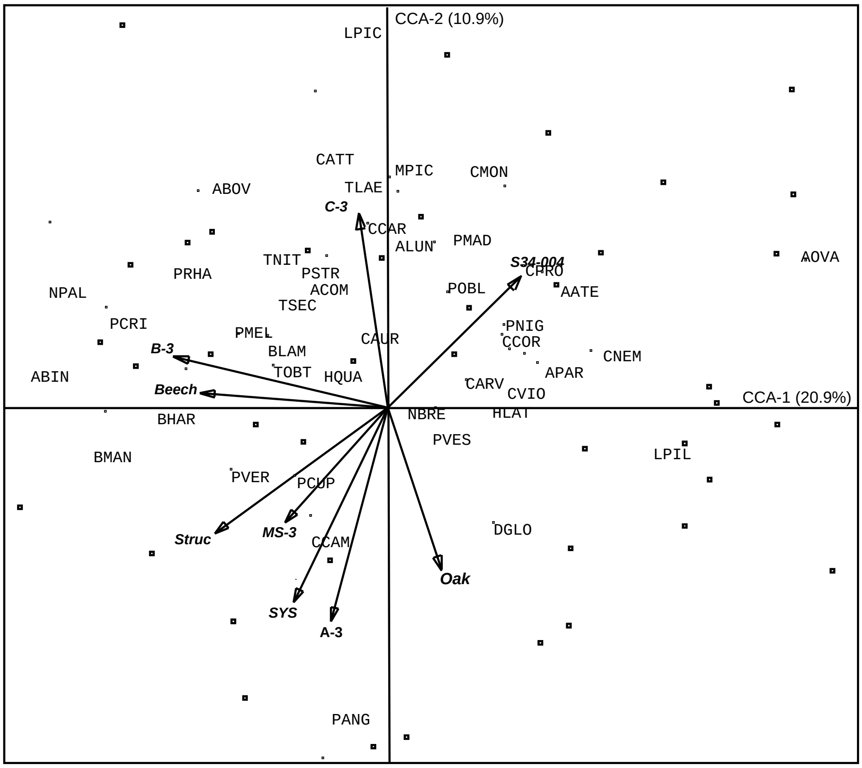


Fig. 4a. Species-variables relationships in young stands: situation of plots (hollow squares), species and variables in the space formed by the two first axes of the CCA performed with management factors as environmental file and other variables as co-variable file (Table 3, step 2). See Table 2 for the codes of variables, and Appendix for the codes of species. Only the significant variables ($p < 0.05$) are presented on the graph.

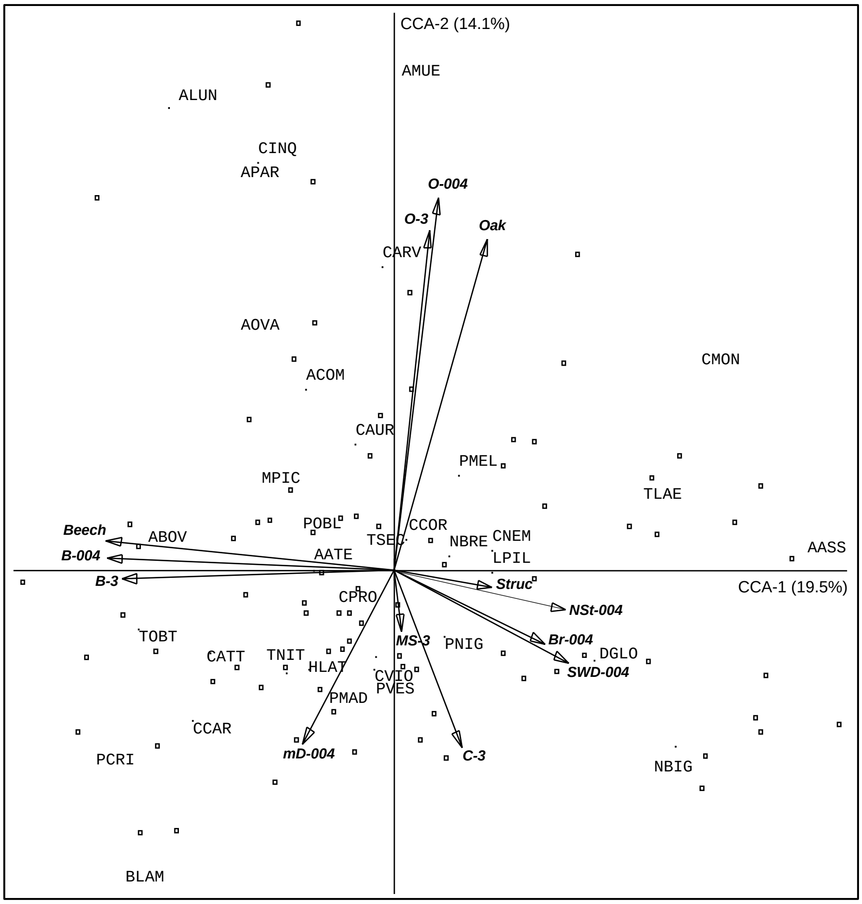
classes clearly differed more in terms of management than in terms of climate and soil (Table 1). In facts, variables such as branch cover, volume of small woody debris and shrub cover were not homogeneous in each sampling class while explaining a significant part of the carabid variation (Table 2). Such variables are neglected when the sampling structure is only related to species assemblages by a single CCA, as frequently done. Theoretically, for applying direct gradient analysis we need to measure the determining environmental variables and to include them in the environmental file (Økland 1996, MacCune 1997); but since these variables are rarely known from the beginning, it is not recommended to restrict the analysis to a limited set of variables, e.g. those chosen for organising the sampling. Care should always be taken when comparing communities only on the basis of simple categorical habitat or management variables. Adding uncontrolled significant variables ($p < 0.05$) increased the explanatory power, which shows that at least some of these variables are ecologically relevant (altitude, branch cover, etc). However, the interactions between sampling structure and uncontrolled variables seem to have non-negligible effects on species assemblages, which suggest that apparent differences between sampling classes (e.g. beech/conifer) may be due to variables not considered in the first CCA. The effect of management should always be evaluated after removing other influences; when not possible, the relationships between both variable groups should be taken into account. This demonstrates the advantage of quantifying the effect of chosen variables independently of others (partial CCA).

The relative importance of management

Our results show that although it is quantitatively limited, the influence of stand age, structure and composition on carabid assemblages is very significant. Other studies also revealed such effects (Baguette and Gérard 1993, Butterfield et al. 1995, Ings and Hartley 1999, Humphrey et al. 1999, Jukes et al. 2001).

We found carabid communities of young stands to be strikingly different from those of medium-aged and mature stands. The particular species assemblages of young stands have been identified by a number of authors (Sustek 1981, Baguette and Gérard 1993, Butterfield et al. 1995, Ings and Hartley 1999, Elek et al. 2001, Heliölä et al. 2001), but the effect of the patch size in young stands has scarcely been studied until now. Our results show its great importance. It seems that even small open spaces in forests (<0.20 ha) can be inhabited by particular carabid communities as suggested by Koivula and Niemelä (2003).

Fig. 4b. Species-variables relationships in medium-aged and mature stands: situation of plots (hollow squares), species and variables in the space formed by the two first axes of the CCA performed with management factors as environmental file and all other factors as co-variable file (Table 3, step 2). See Table 2 for the codes of variables, and Appendix for the codes of species. Only the significant variables ($p < 0.05$) are presented on the graph.



Few species were associated with medium-aged and mature stands in general; most forest species were also present in young stands, albeit in lower abundance (see Appendix). A number of forest species can migrate to nearby open habitats to seek prey during the night (Jukes et al. 2001), and some others can survive in the

Table 4. Species the best and the least explained by all environmental variables. Numbers in brackets indicate the percentage of variation explained by all variables.

	Young	MS[a]	W[b]	Medium-aged and mature	MS[a]	W[b]
Best explained species	*Abax ovalis* (98)	14.0	B	*Cychrus attenuatus* (81)	15.5	B
	Pterostichus madidus (96)	15.0	B	*Carabus coriaceus* (71)	36.0	B
	Cychrus attenuatus (96)	15.5	B	*Carabus violaceus* (67)	25.0	B
	Abax parallelus (95)	16.0	B	*Abax ovalis* (65)	14.0	B
	Pterostichus angustatus (94)	10.3	M	*Agonum assimile* (61)	10.5	M
	Notiophilus palustris (93)	5.5	D	*Carabus arvensis* (55)	18.0	B
	Carabus coriaceus (93)	36.0	B	*Carabus nemoralis* (53)	24.0	B
Least explained species	*Pterostichus melanarius* (60)	15.0	D	*Dyschirius globosus* (17)	2.6	B
	Bradycellus harpalinus (62)	4.0	D	*Pterostichus melanarius* (17)	15.0	D
	Cychrus caraboides (69)	16.5	B	*Cychrus caraboides* (18)	16.5	B
	Bembidion mannerheimi (70)	3.6	D	*Nebria brevicollis* (18)	12.0	M
	Nebria brevicollis (73)	12.0	M	*Trechus secalis* (19)	3.8	B
	Pterostichus strenuus (74)	6.6	D	*Amara ovata* (19)	8.8	M
	Dyschirius globosus (74)	2.6	B	*Agonum muelleri* (22)	8.4	M

[a] Mean size of the species in mm (Lindroth 1974).

[b] Species' wings development (Lindroth 1974): B = brachipteran (inefficient wings); M = macropteran (efficient wings); D = dimorphic species.

shady micro-habitats of the young stands (Niemelä et al. 1992). Conversely, open-habitat species rarely move deep into nearby closed stands (Heliölä et al. 2001), although some of them (e.g. *B. lampros*) can survive in some micro-habitats present in these habitats (Gourov et al. 1999).

Differences in carabid species assemblages between broadleaf and conifer forests were revealed by some authors (Butterfield et al. 1995). Our results illustrate this fact, namely by the CCA graphs where oak, beech and conifer stands are defined by different species. This point was more precisely analysed in du Bus de Warnaffe and Lebrun (2004), based on the same sampling. Two facts could explain that most species of conifer stands are common and unspecialised: 1) conifer forests constitute a relatively recent habitat in southern Belgium; 2) these stands show a low botanical diversity (du Bus de Warnaffe 2002).

How can we interpret the unexplained variation?

Ecological variables rarely explain >60% of the dependent variables studied (Peek et al. 2003). The explained variation was higher in young stands than in older ones. First, past silvicultural practices (not controlled here) may play a less important role in young stands, clear-cutting taking the dominant role by considerably disturbing the community present in the previous stand (Heliölä et al. 2001, Koivula et al. 2002, du Bus de Warnaffe and Lebrun 2004). By contrast, carabid communities of medium-aged and mature stands may depend on past management such as changes in tree composition. Second, shady conditions may decrease the difference between plots in ages 1 and 2. In the corresponding plots the assemblages are clearly dominated by a limited number of species (see Appendix), namely *A. ater*, *C. problematicus* and *P. oblongopunctatus* (generalist and relatively large species) which constitute 86% of the total abundance. By contrast, the three most abundant species in young stands (*A. ater*, *P. versicolor* and *C. problematicus*) only constitute 46% of the total abundance, the other species occurring mostly within strict habitat parameters (patch size, ground cover, altitude, etc.). Moreover, large and generalist species such as *Carabus problematicus* may be particularly subjected to random walk (Nève de Mévergnies and Baguette 1990), defined as movements without clear direction (Baars 1979). We thus suggest that the small-scale population dynamics of the dominant species explains an important part of species assemblage variation in medium-aged and mature stands.

Species little explained by the CCA model with all variables may either be insensitive to the differences between the studied habitats, sensitive to unmeasured variables (e.g. at micro- or macro-scale), or show stochastic distributions. Even with a correct description of habitats and of dispersion/aggregation processes, species abundance may not be predicted with a high probability (Murrell and Law 2000). For example, by definition the random walk of some species cannot be explained by habitat variables or by rules of population dynamics (Baars 1979, Nève de Mévergnies and Baguette 1990) and thus create statistical "noise" (Møller and Jennions 2002). The spatial distribution of abundance can be highly aggregative (Niemelä et al. 1992) and unstable (Tukia and Haila 1992), and related to micro-habitat features on a scale of one metre (Antvogel and Bonn 2001). Moreover, the long-term effects of disturbance on relative species abundance are highly indeterminate (Yodzis 1988).

These developments address the questions of the adequacy between goals, sampling method and statistical tools. First, it seems impossible to rigorously take the spatio-temporal dynamics of the populations into account when data are collected by one-year pitfall trapping without a regular or random grid. However, a number of authors used this method with carabids (Matveev 1992, Baguette and Gérard 1993, Magura et al. 2000, Elek et al. 2001, Heliölä et al. 2001, Kinnunen et al. 2001), even for studies on dispersion (Petit 1994). In any case, ecological conclusions based on local and annual sampling should be drawn with care. Second, even if CCA allows finding the best statistical relationships between species assemblages and site characteristics (ter Braak 1986), it may not reveal real functional links. A positive correlation between a given species and a given habitat feature may indicate either a direct link (use of habitat resources by the species), an indirect link (use by species prey), or even no functional link due to a confusion between inter-correlated variables. As well, a positive correlation between two species may indicate simple co-occurrence due to common life traits, without biotic interaction; a negative correlation between two species may indicate opposite resource needs but also competitive exclusion. We can suppose that co-occurrence and opposite resource needs are present in young stands, while direct and indirect species-habitat links and competitive exclusion take place in mature stands. But our data and the CCA model cannot prove this.

Optimising ordination models

According to Gauch (1982), "replicate community samples" are rarely 100% similar and the variation of species assemblages "incorporates on the order of 10 to 50% noise". Our 15 and 45% of unexplained variation could be noise on the basis of this statement, the rest being "explained" by the variables used. But how to be sure that the 55 and 85% of "explained" variation do not include noise, i.e. that our explanatory variables do not create noise?

The correlation between explanatory variables can create noise, but it is not clear as to whether this effect is important or not with CCA (Palmer 1993 vs MacCune 1997). We however tried to solve this problem. Suppressing one of the variables of each linked couple from the analysis is easy with variables describing the same habitat dimension (e.g. percentage of beech on 0.04 and 0.20 ha), but it may be very difficult in other cases (e.g. tree mean diameter and moss cover: $r = 0.61$, $p < 0.001$). It may not even be logical to eliminate one of them when the two variables express completely different but important aspects of the habitat (e.g. pH and vertical canopy heterogeneity: $r = -0.43$, $p < 0.01$). In this case we chose to keep all significant variables since it was impossible to know which one was the biologically important one (or if both were).

In any case, the stability of models produced by direct gradient analysis is higher with a low number of environmental variables (Prodon and Lebreton 1994). For canonical correlation analysis (CRA) – sharing common properties with CCA – Thorndike proposed that the minimal sample size be 10 times the total number of variables, plus 100 for good measure (Smith 1980), in order to produce results that can be generalised. This idealistic rule has rarely been applied to CCA. Even the scientists who set up CCA used five environmental variables with 20 plots as basic example (Jongman et al. 1987, pp. 139–144). Applying this rule to our case, CCA should simply not be used: with a number of variables ten times the number of sites, we would need to select four variables for young stands and eight for medium-aged and mature stands. But in view of the issues discussed above, how could this selection be done?

It seems very difficult to construct good environment file(s) when no deterministic model is available. A compromise between correct habitat description and stability of regression models should be found. The ideal solution with CCA is to choose the “best” variables from the biological point of view (MacCune 1997), but how to select these variables when the objective of the study is just to describe species-habitat relationships? It is impossible to be sure from the outset that a given variable is or is not biologically relevant. A solution would be to avoid random and worse variables by choosing only habitat variables that seem to be biologically relevant on the basis of scientific literature and/or intuitively, and then to remove by Monte-Carlo tests the variables that are not more correlated with species assemblages than do random ones. This is what we have done here. But even when applying this method, the researcher never knows if some biologically-relevant habitat features have been missed. Only the naturalist’s “field intuition” can help to avoid this problem (Prodon and Lebreton 1994).

These developments cast doubts on the value of performing constrained ordination to “explain” species occurrences, a method now widely used in ecology. Indeed, intercorrelation between environmental variables and random noise will always be problematic in CCA. Direct gradient analysis seems not ideal for exploratory studies, but well fitted for testing precise hypotheses concerning the relationships between assemblages and habitats, based on knowledge concerning ecological processes (Økland 1996). In this case, a small number of variables are used and intercorrelation can be limited.

Conclusion

Methodological implications

Our results demonstrate that choosing the explanatory variables and the way that they are expressed is a crucial step in species-habitat studies, especially with constrained ordinations. The variables used to construct the samples will rarely be sufficient to “explain” species assemblages. Even under homogeneous soil and climate conditions, management is far from being able to explain the whole variation in species assemblages and much will be gained from quantifying the effect of other factors. RDA and CCA are useful tools for quantifying the relationships between sets of explanatory variables and between species assemblages and variable sets.

Constrained ordination techniques are useful to test hypotheses, but using them for exploratory studies will produce wrong results if the exploratory variable set is incomplete or include variable without biological sense. An important effort has to be made to eliminate variables creating noise (e.g. redundant) and whose effects appear to be random. The best CCA will be obtained with a limited set of uncorrelated and biologically well-founded variables, describing all habitat dimensions. But such a set is very difficult to construct under concrete conditions. Increasing sample size should make it possible to use a large number of environmental variables while maintaining good statistical conditions (Møller and Jennions 2002).

When local and annual observations are used, a high proportion of the variation in species assemblages is likely to be uncorrelated with the environmental variables. First, the spatial scale of observations has to be adapted to the territory sizes of the studied species. But even so, population dynamics can induce spatial patterns of abundance which cannot be related to local habitat features. Impact studies rarely use pluri-annual data on a systematic grid, but such data could be of great value for analysing the impact of forest management on invertebrates.

Ecological implications

Though forest management taken alone only explained 30% of the variation in carabid assemblages, stand size in young stands and tree composition in medium-aged and mature stands were clearly identified as major variables. Compared to other types of stands, oak and uneven-aged beech forests are characterised by a high number of specific species. Large clear-cuttings encourage open habitats species.

Our results suggest that carabid communities are essentially influenced by the population dynamics of the dominant species in medium-aged and mature stands, and by temporary and local habitat characteristics in young stands. Quite surprisingly, this implies that foresters may have more control on invertebrate assemblages in young and open stands than in typical closed stands, where only tree composition seems to be very influential and a large part of variation seems to be out of human control, at least at the spatial scales we considered here. But in closed stands invertebrate communities may be affected by long-term changes in management. Studies on this topic could be of great value for sustainable forest management.

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Appendix. List of species, relative abundance in young stands (stage 1) and in medium-aged and mature stands (stages 2 and 3) and total number of indidivual recorded (128 plots). Species names are in accordance with the nomenclature of the Belgian Royal Society of Entomology (Coulon 1995).

Species	Code	Stage 1 (%)	Stages 2+3 (%)	Total abondance
Abax ater	AATE	18.46	35.51	11073
Abax ovalis	ABOV	1.31	1.71	542
Abax parallelus	APAR	1.44	0.18	163
Agonum assimile	AASS	–	0.11	32
Agonum muelleri	AMUE	–	0.01	4
Amara communis	ACOM	4.41	0.04	367
Amara lunicollis	ALUN	0.93	0.02	80
Amara ovata	AOVA	0.04	0.01	6
Anisodactylus binotatus	ABIN	0.26	–	21
Bembidion lampros	BLAM	4.30	0.03	356
Bembidion mannerheimi	BMAN	0.12	–	10
Bradycellus harpalinus	BHAR	0.36	–	29
Calosoma inquisitor	CINQ	–	0.05	12
Carabus arvensis	CARV	2.68	0.30	292
Carabus auronitens	CAUR	0.58	0.27	115
Carabus coriaceus	CCOR	2.41	1.08	468
Carabus monilis	CMON	0.10	0.03	15
Carabus nemoralis	CNEM	0.69	0.93	299
Carabus problematicus	CPRO	12.53	30.72	8841
Carabus violaceus	CVIO	2.00	0.91	393
Cicindella campestris	CCAM	0.16	–	13
Cychrus attenuatus	CATT	1.87	3.27	984
Cychrus caraboides	CCAR	0.17	0.02	20
Dyschirius globosus	DGLO	0.27	0.02	26
Harpalus latus	HLAT	0.66	0.05	67
Harpalus quadripunctatus	HQUA	1.07	–	88
Leistus piceus	LPIC	0.07	–	10
Loricera pilicornis	LPIL	0.04	0.02	8
Molops piceus	MPIC	0.10	0.04	17
Nebria brevicollis	NBRE	0.12	0.23	243
Notiophilus biguttatus	NBIG	–	0.18	49
Notiophilus palustris	NPAL	0.12	–	10
Pterostichus angustatus	PANG	0.09	–	8
Pterostichus cristatus	PCRI	0.07	0.05	53
Pterostichus cupreus	PCUP	0.36	–	33
Pterostichus madidus	PMAD	4.20	2.57	1514
Pterostichus melanarius	PMEL	0.10	0.02	15
Pterostichus niger	PNIG	4.18	1.45	706
Pterostichus oblongopunctatus	POBL	11.64	19.68	5995
Pterostichus rhaeticus	PRHA	0.09	–	8
Pterostichus strenuus	PSTR	0.36	–	29
Pterostichus vernalis	PVER	0.10	–	10
Pterostichus versicolor	PVES	15.44	0.02	1252
Trechus obtusus	TOBT	1.25	0.18	152
Trechus secalis	TSEC	3.46	0.14	315
Trichotichnus laevicollis	TLAE	0.42	0.07	59
Trichotichnus nitens	TNIT	0.95	0.09	104
Total	–	100.00	100.00	34906