

Effects of forest management on carabid beetles in Belgium: implications for biodiversity conservation

Gaëtan du Bus de Warnaffe ^{a,*}, Philippe Lebrun ^b

^a *Unité des eaux et forêts, Centre de recherches sur la biodiversité, Université catholique de Louvain, Louvain-la-Neuve 1348, Belgium*

^b *Unité d'écologie et de biogéographie, Centre de recherches sur la biodiversité, Université catholique de Louvain, Louvain-la-Neuve 1348, Belgium*

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Abstract

We sampled the carabid beetles in 22 forests managed by six different silvicultural systems, defined by treatment and tree species composition: even-aged conifer, even-aged beech, even-aged oak, uneven-aged conifer, uneven-aged beech and group mixed (beech + conifer). In each of these forests, we placed pitfall traps in young, medium-aged and mature stands (3 stages). We evaluated the effect of treatment, tree species composition, silvicultural system, stage and habitat type (silvicultural system + stage) on indicators of community conservation value and ecological structure. The species composition and the ecological structure of carabid beetles of the managed stands were then compared to that of nine unmanaged stands (without tree exploitation). In the managed forests, species richness was highest in large young stands (3–10 years old) and in forests managed by even-aged systems (with large clear-cuts), mainly due to eurytopic and opportunist carabid species with high dispersal abilities. Oak and beech, uneven-aged, and mature stands were mainly inhabited by typical forest species, and even-aged conifer stands mainly by ubiquitous species. Several typical forest species recorded in unmanaged stands were lacking from the managed forests. Large scale clear-cutting allows open-habitat species to enter the forest, which increases the species richness at a landscape level but can disfavour typical forest species by competition. Long rotations should be implemented and more areas left unmanaged in Belgium, in order to help typical forest species to re-colonise managed forests.

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1. Introduction

In natural forests, ecological processes are driven by frequent biological changes, resulting from disturbances such as storms, floods, fires and landslides (Attiwill, 1994; Peterken, 1996). These disturbances produce a dynamic mosaic pattern of patches at different stages of the ecological succession, leading to a high diversity of habitats (Pickett and White, 1985). Such natural disturbances are partially controlled in forests managed for wood production. However, management itself produces a complex mosaic in forests (Wigley and Roberts,

1997; Lertzman and Fall, 1998) and creates new habitats (e.g. clear-cuttings), which can be beneficial to some species threatened by the intensification of agricultural practices (Baguette, 1993; Niemelä et al., 1993; Heliölä et al., 2001). Management can undoubtedly influence processes and communities in forests (Christensen and Emborg, 1996), but the conservation impacts of these changes remain a complex issue.

Several studies have been conducted with insects on this topic. They point out the effect of clear-cutting (Sustek, 1981; Niemelä et al., 2000) and the importance of stand age (Day and Carthy, 1988; Ings and Hartley, 1999; Koivula et al., 2002), composition (e.g. Fahy and Gormally, 1988) and structure (Magura et al., 2000; Jukes et al., 2001). However, the ecological impact of silvicultural systems results from combining the effect of these factors (Matthews, 1996; Malcolm et al., 2001). All stages of the silvicultural cycle have to be considered to

* Corresponding author. Present address: UMR Dynamiques forestières dans l'espace rural, Institut National de la Recherche Agronomique, Chemin de Borde Rouge, BP 27, Castanet-tolosan 31326, France. Tel.: +33-561.28.53.39; fax: +33-561.28.54.11.

E-mail address: gdubus@toulouse.inra.fr (G. du Bus de Warnaffe).

allow a broad assessment of a management system. Recent studies generally follow this last principle, but few of them compare the broad impact of different silvicultural systems, though it would be very informative for managers.

To solve this problem, we chose: (1) Several important Belgian silvicultural systems. (2) Two spatial levels for the description of species assemblages: (a) plots of a given growth stage, and (b) forest areas integrating the major stages of the silvicultural cycle. (3) The coleopteran family of carabid beetles as indicator of forest insect diversity (Butterfield et al., 1995). As most species of this group are ground dwellers in the adult stage, soil dwellers in the immature stages and active predators, carabids are very sensitive to the changes in their environment (e.g. Thiele, 1977; Niemelä et al., 1992; Baguette, 1993; Niemelä et al., 2000). Moreover, they include many forest-specific species, which can form dense populations in forests. (4) A system of indicators allowing us to interpret the species data in a conservation perspective. (5) Several unmanaged forests for comparison with the managed areas.

The conservation value of the communities was quantified by four complementary criteria: richness, rarity, specificity and integrity (Kirkpatrick and Gilfedder, 1995; du Bus de Warnaffe and Devillez, 2002). We described the ecological structure of the communities to relate conservation value to community functioning, in order to propose valuable recommendations for management.

2. Methods

2.1. Study region, silvicultural systems and experimental design

The study took place in the region of the Ardennes (southern Belgium), which is mostly composed of pastures and woodlands, partially transformed over the last 150 years into commercial conifer stands (Devillez and Delhaise, 1991). The Ardennes are characterised by a humid sub-mountainous climate, gentle 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). The tree species covering the forests being studied were mostly spruce (*Picea abies* (L.) Karst), Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), beech (*Fagus sylvatica* L.), and oak (*Quercus petraea* (Mattme.) Liebl. and *Quercus robur* L.). All the sites were located on *Luzulo-Fagetum* or *Luzulo-Quercetum* potential vegetation according to the phytosociological system of Noirfalise (1984), on flat or very slightly sloping ground of acid brown and moderately dry soil (*Dystric cambisol*: FAO, 1990).

In western Europe, silvicultural systems can be characterised by two major variables: (1) size of the patches produced by logging mature trees (clear-cuttings), i.e., ‘treatment’, and (2) major tree species or ‘composition’. Treatment actually determines the ‘grain of heterogeneity’ (Kotliar and Wiens, 1990; Hansson, 1992), which managers generally characterise by the difference between even-aged (large clear-cuttings, coarse-grained) and uneven-aged (small clear-cuttings, fine-grained) forests. We studied the six most common silvicultural systems in the Belgian Ardennes, defined by the treatment (first initial) and by the composition (second initial): (1) even-aged conifer (EC): forests regenerated by large clear-cuttings (>2 ha), and where spruce and/or Douglas fir have >80% cover; (2) even-aged beech (EB): forests regenerated by large clear-cuttings (>2 ha), and with beech >80%; (3) even-aged oak (EO): forests regenerated by large clear-cuttings (>2 ha), and with oak >80%; (4) uneven-aged conifer (UC): forests regenerated by small clear-cuttings (<0.2 ha), and with spruce and/or Douglas fir >80%; (5) uneven-aged beech (UB): forests regenerated by small clear-cuttings (<0.2 ha), and with beech >80%; (6) group mixed (GM): forests regenerated by medium-sized clear-cuttings (0.2–0.5 ha), and with spruce and/or Douglas fir 25–75%, the rest being covered by beech.

Three to five forest areas of about 15 ha were chosen to represent each silvicultural system. The mean size of the clear-cuttings and the tree species composition were evaluated from aerial photographs by GIS.

Integrating the temporal dimension of the silvicultural cycle can be performed by studying simultaneously the major stages of the cycle in a given forest area (space for time substitution). Three stages were identified: clear-cuttings or ‘regeneration stage’ (stage 1: trees 3–10 years old), medium-aged stands (stage 2: 20–40 years old for conifer stands, 30–60 years old for broadleaf stands), and mature stands (stage 3: 50–80 years old for conifer, 80–140 years old for broadleaf). In each forest area, we selected six plots of 0.04 ha: two in stage 1, two in stage 2 and two in stage 3. Field measurements showed that the vertical heterogeneity of the canopy was significantly higher in uneven-aged forests than in even-aged ones. Consequently, treatment defines the size of the clear-cutting in stage 1 (large/small), and the vertical heterogeneity of the canopy in stages 2 and 3 (even-aged/uneven-aged).

We kept a minimum distance of 100 m between any two sample plots and 100 m to the nearest crop or meadow. The 6 × 3 = 18 silvicultural system/stage combinations were called ‘habitat types’. In all, 22 forest areas and 128 plots were selected (Table 1).

2.2. Carabid beetle sampling

We used 8.5 cm × 17 cm pitfall traps with 5% formaldehyde to collect ground-dwelling arthropods (Dufrêne,

Table 1
Number of forest areas per silvicultural system and number of plots per habitat type

Forest treatment	Even-aged			Group	Uneven-aged		Total
	Conifer	Beech	Oak ^b		Mixed	Conifer	
Number of forest areas	4	3	3 + 1	3	3	5	21 + 1
Number of plots by stage ^a							
Stage 1	8	6	6	6	5	10	41
Stage 2	8	6	6	6	7	10	43
Stage 3	8	6	6 + 2	6	6	10	44
Total number of plots	24	18	20	18	18	30	128

^a Stage 1, regeneration stage; stage 2, medium-aged stage; stage 3, mature stage.

^b In one of the oak forest areas chosen, we placed only two plots in stage 3.

1988). In each plot, three pitfalls were placed in an equilateral triangle of 3 m side (Desender et al., 1999) and emptied at monthly intervals (Heliölä et al., 2001) from 10 April to 5 November 1999 (Düldge, 1994). Identification of the carabids was principally carried out with the help of Lindroth's keys (Lindroth, 1974), according to the nomenclature of the Belgian Royal Society of Entomology (Coulon, 1995); authorities are given in Table 7. For the forest areas (integrating stages 1, 2 and 3), the species/site table was obtained by summing the individuals collected in the six plots of each forest area, for each carabid species.

Catches with pitfalls can be used to estimate the density of carabid beetles (Baars, 1979), but as mentioned by several authors (e.g. Niemelä et al., 1993; Kinnunen et al., 2001), they are better adapted for comparing species richness and abundance levels (total and by species) between habitats – which is the case here.

2.3. Data on unmanaged stands

We used data on nine unmanaged stands situated in ecologically similar conditions (climate, soil, vegetation), 80–300 km from the managed ones: the strict reserve of Rognac and the beech reserve of Rurbusch in Belgium; the beech forests of Conventenwald, Wilder See and Napf and the oak forests of Bechter Wald and Sommerberg in south-west Germany and the beech forests of Schäferheld and Wiegelkammer in western Germany. The data on these stands have already been published in

academic reports (du Bus de Warnaffe, 2002; Vast, 2001; Bücking, 1998; Köhler, 1996). All stands were situated in the south-west of the Centro-European biogeographical Domain (Ozenda, 1994) and in similar potential vegetation types (Table 2). The sampling methods used were the same as in our managed stands, but the number of trapping months varied from 7 to 20 as compared to 7 in managed stands (Table 2).

2.4. Data analysis

2.4.1. Conservation value

Species richness (number of carabid species collected in each plot or forest area) was used as first indicator of the conservation value. According to two different methods based on accumulation curves for the seven months and three pitfalls per plot (Ferry, 1976; Lauga and Joachim, 1987), species exhaustiveness was high: >91% for the plots, >97% for the forest areas and >98% for the habitat types and for the silvicultural systems. Thus, we can reasonably suppose that the probability of having missed species is very low and therefore, that the sampling efforts in managed and unmanaged stands are comparable.

Rarity was measured for each plot and each forest area by weighted species richness, according to Bezzel (1980) and Eyre and Rushton (1989), based on summing the individual conservation value of each species (Csp) recorded in the unit. Recent data available for southern Belgium (OFFH, 2001) were used to calculate Csp, by:

Table 2
Major characteristics of the unmanaged stands

Authors	Vegetation type	Major tree species	Number of . . .			Alt. (m)	Dead wood	Area (ha)
			Forests	Traps	Months			
du Bus de Warnaffe (2002) ^a	<i>Luzulo-Fagetum</i>	Beech, Oak, Birch	1	18	7	210–220	19.5 m ³ /ha	11
Vast (2001) ^a	<i>Luzulo-Fagetum</i>	Beech (+Spruce)	1	50	8	530–610	50 m ³ /ha	49
Bücking (1998) ^b	<i>Luzulo-Fagetum</i>	Beech	3	21	20/13	730–1280	37.5 m ³ /ha	17–65
Bücking (1998) ^b	<i>Stellario-Carpinetum</i>	Oak, Hornbeam, Beech	2	30	20	170–390	50.5 m ³ /ha	13 and 43
Köhler (1996) ^b	<i>Luzulo-Fagetum</i>	Beech	2	8	14	370–530	10% m ³	13 and 24

^a Stands in Belgium.

^b Stands in western Germany.

$$Csp = (\text{rarity} \times \text{tendency})/20,$$

where rarity = 1–10 according to the numbers of UTM squares of southern Belgium where the species is present, and tendency = 2 for species in significant decline at the regional level and 1 for other species.

Species richness and weighted species richness were not computed for the unmanaged stands, since the number of pitfalls per site were not equal to that of managed stands.

The *specificity* of the community for a given habitat or forest type can be defined as the number of species statistically more frequent and more abundant in this type (Dufrêne and Legendre, 1997). The necessary lists of species are not yet available for carabids, but since our sampling covers nearly all the habitat types found in Belgian Ardennes forests, we used our data (128 plots, >34,000 individuals) to construct this list.

Specificity of species *i* to the group of sites *j* = (mean abundance of the species *i* per site in the group *j*) / (mean abundance of the species *i* per site in the whole sample).

We used simple non-hierarchical typologies of samples for the plot and the forest areas. For forest areas, we used a first typology based on the treatments (even-aged, group, uneven-aged) and a second based on the silvicultural systems. Typology based on composition brought few results. For the plots, we simplified the classification (18 classes) on the basis of a correspondence analysis. This brought two successive typologies: a first one with three classes (large clear-cuttings, medium clear-cuttings and all other plots), and a second with four classes excluding the large and medium clear-cuttings (UB1-3, EO2-3, EB2-3 and EC2-3 + UC1-3), separating the plots of the GM system in the last two classes according to their local composition. For both plots and forest areas, species were defined as specific when showing specificity >50% for one of the classes of the typology, providing they were present in at least two plots or forest areas of this class. Species showing specificity >70% were considered as very specific.

The *integrity* of the carabid community (Angermeier and Karr, 1994) was estimated using the list of species present in the unmanaged stands situated in similar ecological conditions (see Section 2.3).

2.4.2. Ecological structure of the communities

We used the profile of habitat preferences to study the ecological structure of the carabid communities. We simplified the classification of Desender et al. (1995) into the four major categories recorded: stenotopic forest species, eurytopic forest species, open-habitat species and ubiquitous species. The number of individuals was used as basic data. Special attention was paid to the representation of

forest stenotopic species, since these are competitors generally depending on large and only slightly disturbed forests (Desender et al., 1999). Finally, the percentage of individuals belonging to macropterous species was computed as a mean to quantify the colonisation abilities of the carabid community (Ribera et al., 2001).

2.4.3. Statistical tests

Analysis of each indicator was undertaken for the plots (single stage) and the forest areas (stages 1 + 2 + 3). For all indicators except specificity, we drew two-dimensional graphs and made non-parametric Kruskal–Wallis tests (KW: Sokal and Rohlf, 2000) with the SAS package, to evaluate the significance of the effects of treatment, composition, silvicultural system (treatment + composition), stage, and habitat type (treatment + composition + stage).

3. Results

3.1. Conservation value

3.1.1. Plot analysis (one stage)

3.1.1.1. Species richness. In all, 34,906 individuals belonging to 65 carabid species were collected (see Table 7). When the whole sample was taken into consideration (128 plots), treatment, composition, stage, silvicultural system and habitat type all showed strong effects on species richness (Fig. 1a and Table 3, first column). *Treatment* of forests significantly affected species richness only in stage 1 (Table 3a). Since the clear-cuttings in the UC system were very small (often <0.04 ha), our results suggest that only clear-cutting >0.04 ha can increase carabid species richness, but that above this limit, the effect of clear-cutting size is weak (stages 1 of other systems have comparable levels, see Fig. 1a). The *composition* of the forests influenced species richness only in stage 3 (mature stands, Table 3b). The effect of the *stage* of the stand was expressed by the clearly higher species richness in stage 1 than in stages 2 and 3, except in EO and UC systems (Fig. 1a and Table 3c). *Silvicultural system* and *habitat type* both strongly influenced the species richness (Table 3d).

3.1.1.2. Rarity: weighted species richness. When the whole sample was analysed, treatment, composition, stage, silvicultural system and habitat type all significantly affected the weighted species richness (Table 3, first column). *Treatment* had a significant impact at stage 1 of conifer forests (even-aged > uneven-aged), but no significant impact appeared in stages 2 and 3 (Table 3a). The impact of *composition* was stronger in stages 2 and 3 than in stage 1 (Table 3b and Fig. 1b), with weighted species richness in oak one-and-a-half times to twice that

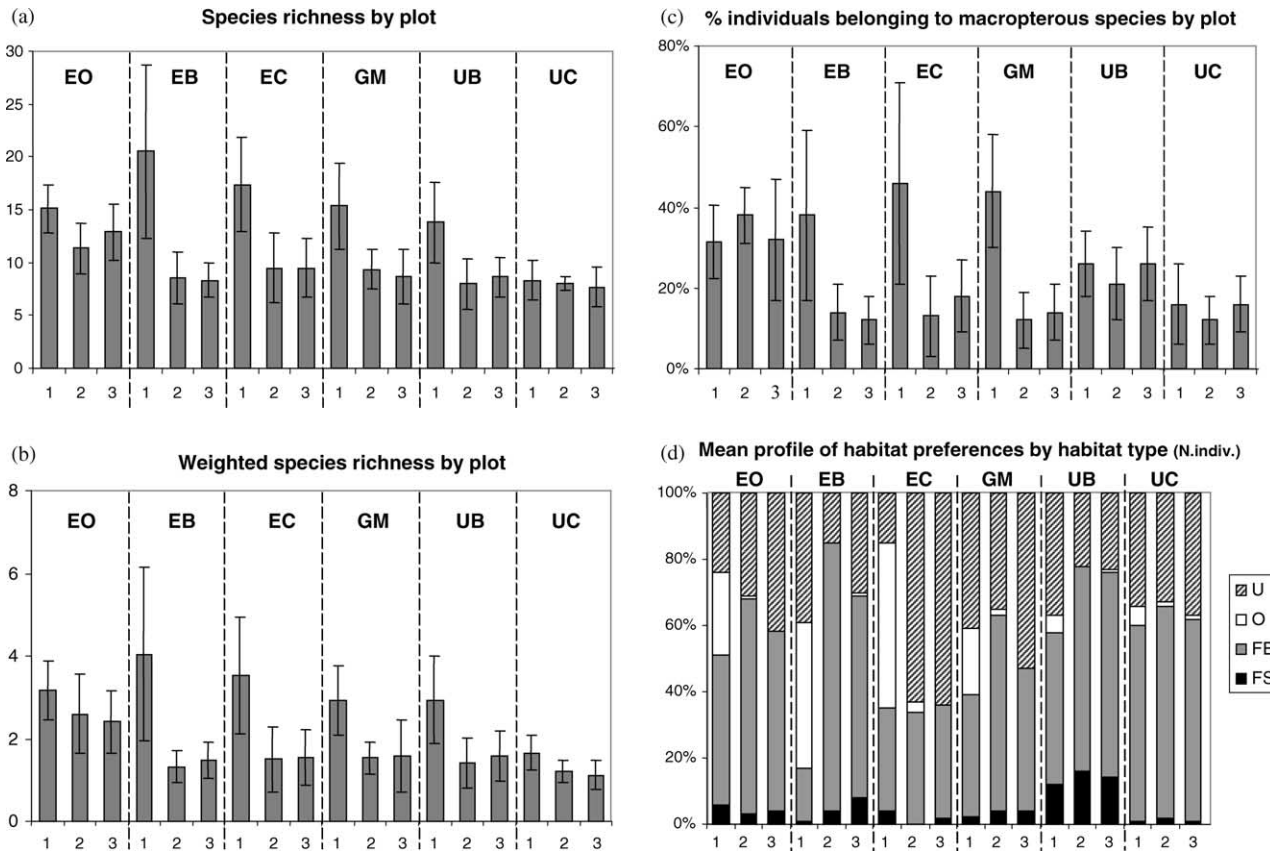


Fig. 1. Mean and standard deviation of indicators of conservation value (a,b) and indicators of ecological structure (c,d) of carabid communities by habitat type (128 plots). Silvicultural systems: EO, even-aged oak; EB, even-aged beech; EC, even-aged conifer (spruce + Douglas fir); GM, group mixed; UB, uneven-aged beech; UC, uneven-aged conifer. Growth stages: 1, regeneration; 2, medium-aged; 3, mature. Habitat preferences (d): U, ubiquitous species; O, open-habitat species; FE, eurytopic forest species; FS, stenotopic forest species.

of other compositions. Higher values were obtained in stage 1 than in older stages (Fig. 1b and Table 3c), except in oak forests and in UC forests – where the clear-cuttings were very small. The impacts of *silvicultural system* and *habitat type* were both significant (Table 3d).

3.1.1.3. Specificity. Large clear-cuttings showed a high number of specific species (Table 5), but five species were specific to medium-size clear-cuttings and ten to other habitat types. Stands of EO and UB systems contained several specific species, whereas only *Agonum assimile* was specific to conifer stands and no specific species was found for EB stands.

3.1.2. Forest area analysis (stages 1 + 2 + 3)

3.1.2.1. Species richness. Species richness was strongly influenced by *treatment* and by *silvicultural system*, even-aged systems showing about 10 species more, in broadleaf and in conifer forests (Table 4 and Fig. 2a). Though broadleaf systems seemed to have more species, the effect of *composition* was not significant, even when the treatments were analysed separately (Table 4).

3.1.2.2. Rarity: weighted species richness. The weighted species richness was influenced by *treatment* only in conifer forests (even-aged > uneven-aged), and *composition* had no significant impact (Table 4 and Fig. 2b).

3.1.2.3. Specificity. Even-aged systems had a particularly high number of specific species (Table 6), due to the attractiveness of clear-cuttings for non-forest species (Table 5). However, five species were specific to UB forests, mostly stenotopic dwellers which demand minimally disturbed environments (Desender et al., 1999) and are quite rare at the regional level (OFFH, 2001).

3.1.2.4. Integrity: species lacking from the managed stands. Fifty-one species were common to managed and unmanaged stands and 14 species were only found in the managed stands, most of them open-habitat species which were best represented in stage 1 (clear-cuttings).

Twenty-three carabid species were found only in the unmanaged stands (Table 7). Most of them are forest dwellers, and 14 of these species were also identified by Bücking (1998) and Köhler (1996) as twice as abundant

Table 3

Plot analysis. Significant levels of the tests concerning the effects of (a) forest treatment, (b) composition, (c) stand age, and (d) silvicultural system and habitat type (H.T.) on species richness, weighted richness and profile of habitat preferences

(a) Sample part (composition/stage)	All	1	2	3	Beech				Conifer			
					All	1	2	3	All	1	2	3
Species richness by plot	**	**		°		°			***	**		
Weighted species richness	*	°							*	*		
% of stenotopic forest species	**	°	°	°	**	*	*		°		°	
% of eurytopic forest species	*	*		*		***			***	°	**	**
% of ubiquitous species	°	**	***	***					***	*	**	**
% of species of open habitats	*	***				**				**		°
% of macropterous		**			**	*	*	*	*	*		
(b) Sample part (treatment/stage)	All	1	2	3	Even-aged				Uneven-aged			
					All	1	2	3	All	1	2	3
Species richness by plot	*		°	**				*	*	**		
Weighted species richness	*		*	*	°		*	*	*	*		°
% of stenotopic forest species	***	*	**	**	*		*	*	***	**	*	**
% of eurytopic forest species	°		*	°	***	*	***	*				*
% of ubiquitous species	***		***	**	*		***	*	°			*
% of species of open habitats						°						
% of macropterous	*	°	***	*	*		**	°	*	*	°	*
(c) Sample part	All	EB	EC	EO	UB	UC	GM					
Species richness by plot	***	**	**	°	***		*					
Weighted species richness	***	**	**		**	°	**					
% of stenotopic forest species				*								
% of eurytopic forest species	***	**					*					
% of ubiquitous species	*		***	*	*		*					
% of species of open habitats	***	**	***	***	*	°	**					
% of macropterous	**	*	*	*			**					
(d) Tested effect	Silvicultural system				H.T.							
Sample part	All	1	2	3	All							
Species richness by plot	***	**		*	***							
Weighted species richness	**	*	°	*	***							
% of stenotopic forest species	***	*	**	**	***							
% of eurytopic forest species	***	**	***	***	***							
% of ubiquitous species	***	*	***	**	***							
% of species of open habitats		***			***							
% of macropterous	*	**	**	*	***							

Kruskal–Wallis tests were performed on the whole sample ('All', 128 plots) or on successive parts of it ('sample part'). For instance, the P value characterising the effect of treatment on species richness is worth 0.001 in general and >0.2 in mature stands of beech forests. Modalities of treatment, composition and silvicultural system are defined in Section 2.1 of the text; stages 1, 2 and 3 summarise the silvicultural cycle.

Blanks: $P > 0.1$; ° $0.05 < P < 0.1$; * $0.01 < P < 0.05$; ** $0.001 < P < 0.01$; *** $P \leq 0.001$.

Table 4

Forest area analysis. Significant levels of the tests concerning the effects of forest treatment, composition and silvicultural system on species richness, weighted richness, profile of habitat preferences and percentage of individuals belonging to macropterous species

Tested effect	Treatment			Composition			Silv. system
	All	Beech	Conifer	All	Even-aged	Uneven-aged	
Sample part	All	Beech	Conifer	All	Even-aged	Uneven-aged	All
Species richness by forest area	***	*	*				*
Weighted species richness	**	°	*			°	*
% of stenotopic forest species						°	
% of eurytopic forest species			*		°		°
% of ubiquitous species	*		*	*	*		*
% of species of open habitats	**	°	*				*
% of macropterous			°			*	

Kruskall–Wallis tests were performed on the whole sample ('All', 22 forest areas) or on successive parts of it ('sample part'). Classes of treatment and composition are defined in Section 2.1 of the text. For instance, the *P* value characterising the effect of treatment on species richness is ≤ 0.001 in general and < 0.05 in conifer forests.

Blanks: $P > 0.1$; ° $0.05 < P < 0.1$; * $0.01 < P < 0.05$; ** $0.001 < P < 0.01$; *** $P \leq 0.001$.

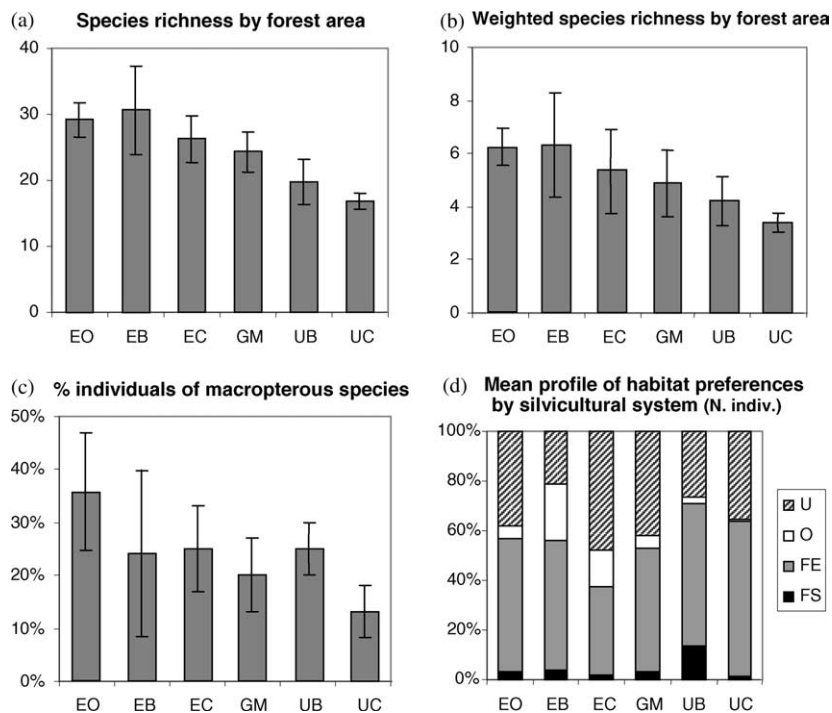


Fig. 2. Mean and standard deviation of indicators of conservation value (a,b) and indicators of ecological structure (c,d) of carabid communities by silvicultural system (22 forest areas). Silvicultural systems: EO, even-aged oak; EB, even-aged beech; EC, even-aged conifer (spruce + Douglas fir); GM, group mixed; UB, uneven-aged beech; UC, uneven-aged conifer. Habitat preferences (d): U, ubiquitous species; O, open-habitat species; FE, eurytopic forest species; FS, stenotopic forest species.

in unmanaged stands as in managed ones (column “U > 2E” in Table 7).

Belgian reserves were characterised by only two species not recorded in managed stands: *Pterostichus diligens* and *Pterostichus nigrita* (Table 7). But according to Bücking (1998) and Köhler (1996), only *P. nigrita* prefers natural woodlands (column “U > 2E”). Hence, the difference between the selected managed and unmanaged stands within the Ardennes was small. However, 19 of the 21 species only found in German unmanaged stands are still

present in Belgium and 18 are still present in the Ardennes, according to recent data (OFFH, 2001). But thirteen of these species are rare in south-Belgium and five are in significant decline at the regional level.

3.2. Ecological structure of the communities

3.2.1. Plot analysis (one stage)

The profile of habitat preferences (Fig. 1d) was strongly influenced by treatment, composition, stage,

Table 5

Specific species for each group of habitat types, based on Dufrene and Legendre's definition of specificity (Dufrene and Legendre, 1997) (see text, Section 2.4.1). See Table 7 for the complete names of species

(Group of) habitat type(s)	N^a	Very specific ($S > 70\%$)	Specific ($50 < S < 70\%$)	N_{ssp}^b
Large clear-cuttings (>2 ha)	18	<i>Bembidion mannerheimi</i> <i>Dyschyrius globosus</i> <i>Pterostichus madidus</i> ^c <i>Pterostichus versicolor</i> ^c <i>Pterostichus vernalis</i> <i>Trechus secalis</i>	<i>Abax parallelus</i> <i>Amara communis</i> <i>Amara lunicollis</i> <i>Carabus arvensis</i> <i>Carabus auratus</i> <i>Cicindella campestris</i>	12
Medium clear-cuttings (0.2–0.5 ha)	6	<i>Pterostichus rhaeticus</i>	<i>Bembidion lampros</i> <i>Carabus coriaceus</i> <i>Carabus violaceus</i> * <i>Pterostichus niger</i> *	5
Small clear-cuttings (<0.2 ha) and stages 2 and 3 of all systems	104	<i>Abax ater</i> ^c <i>Carabus problematicus</i> ^c <i>Pterostichus oblongopunctatus</i> ^c <i>Abax ovalis</i> <i>Cychrus attenuatus</i> <i>Notiophilus biguttatus</i> <i>Pterostichus cristatus</i> <i>Trichotichnus nitens</i>	<i>Carabus nemoralis</i> <i>Molops piceus</i>	10
Even-aged beech stands (stages 2 and 3)	35	–	–	0
Uneven-aged beech stands (stages 2 and 3) and small clear-cuttings in beech forests		<i>Synuchus nivalis</i>	<i>Cychrus attenuatus</i> <i>Molops piceus</i> <i>Trichotichnus nitens</i>	4
Even-aged oak stands (stages 2 and 3)	14	<i>Calosoma inquisitor</i> <i>Pterostichus cristatus</i>	<i>Abax parallelus</i> <i>Nebria brevicollis</i> <i>Carabus nemoralis</i> *	5
Spruce-douglas fir stands (stages 2 and 3)	37	<i>Agonum assimile</i>	–	1

^a Number of plots of the class.

^b Total number of specific species ($S > 50\%$).

^c Species also found in > 70% of the plots of the corresponding class.

silvicultural system and habitat type (Table 3, first column). The effect of *treatment* was strong in stage 1, with a higher representation of open-habitat species in large and medium clear-cuttings. In conifer stages 2 and 3, ubiquitous species were significantly better represented in even-aged stands, and in beech forests there were significantly more forest stenotopic species in uneven-aged stands (Table 3a and Fig. 1d). In these stages, the effect of *composition* was strong, with a higher representation of ubiquitous species in conifer stands (Table 3b). The effect of *stage* on the profile was marked, but no clear difference appeared between stages 2 and 3.

In even-aged and group systems, the percentage of individuals belonging to macropterous species was clearly higher in stage 1 than in stages 2 and 3 (Fig. 1c and Table 3c); the small clear-cuttings (< 0.20 ha) showed similar macropterous proportions to their nearby stands. In stages 2 and 3, there were significantly more macropterous in oak stands than in conifer ones (Table 3b), and the effects of *treatment* was only significant in beech stands (Table 3a).

3.2.2. Forest area analysis (stages 1 + 2 + 3)

The *treatment* clearly influenced the profile of habitat preferences in conifer forests, with higher representation of open-habitat species and ubiquitous species in even-aged forest (Table 4 and Fig. 2d). The *composition* was influential in even-aged forest, where there was a lower representation in beech forests than elsewhere. Individuals of macropterous species were more abundant in EO forests and were very scarce in UC forests (Fig. 2c), but significant effects were only found for *composition* in uneven-aged forests (Table 4).

3.2.3. Comparison between managed and unmanaged stands

Compared to the managed stands, all the unmanaged stands except Sommerberg and Rognac, showed a high representation of forest species. Napf had a very high percentage of forest stenotopics, mostly due to *Abax ovalis*, *Carabus auronitens*, *Molops elatus*, *Pterostichus burmeisteri* and *Pterostichus pumilio*. More than 70% of the carabids caught at Rurbusch belonged to forest

Table 6

Specific species for each type of forest area, based on Dufrene and Legendre's definition of specificity (Dufrene and Legendre, 1997) (see text, Section 2.4.1). See Table 7 for the complete names of species

Type of forest area	N^a	Very specific ($S > 70\%$)	Specific ($50 < S < 70\%$)	N_{ssp}^b
Even-aged (E)	10	<i>Amara communis</i> ^c <i>Amara lunicollis</i> ^c <i>Abax parallelus</i> ^c <i>Bradycellus harpalinus</i> <i>Bembidion lampros</i> ^c <i>Bembidion mannerheimi</i> <i>Carabus arvensis</i> ^c <i>Cicindella campestris</i> <i>Nebria brevicollis</i> ^c <i>Pterostichus cupreus</i> <i>Pterostichus madidus</i> ^c <i>Pterostichus strenuus</i> <i>Pterostichus vernalis</i> <i>Pterostichus versicolor</i> ^c <i>Trechus secalis</i>	<i>Harpalus latus</i> ^c <i>Notiophilus biguttatus</i> <i>Trichotichmus laevicollis</i> <i>Trechus obtusus</i>	19
Uneven-aged and group (U– + G–)	11	<i>Molops piceus</i> <i>Trichotichmus nitens</i>	<i>Abax ater</i> ^c <i>Cychrus attenuatus</i> <i>Carabus violaceus</i> ^c <i>Harpalus quadripunctatus</i> <i>Loricera pilicornis</i> <i>Pterostichus rhaeticus</i>	8
Group mixed	3	–	<i>Carabus monilis</i> <i>Bembidion lampros</i>	2
Even-aged beech	3	–	<i>Amara lunicollis</i> ^c <i>Bradycellus harpalinus</i>	3
Even-aged spruce-douglas fir	4	<i>Agonum assimile</i>	<i>Carabus arvensis</i> ^c <i>Notiophilus biguttatus</i> ^c	3
Even-aged oak	3	<i>Calosoma inquisitor</i> ^c	<i>Abax parallelus</i> ^c <i>Trichotichmus laevicollis</i>	3
Uneven-aged beech forests	5	<i>Abax ovalis</i> ^c <i>Synuchus nivalis</i> <i>Trichotichmus nitens</i>	<i>Cychrus attenuatus</i> ^c <i>Molops piceus</i> ^c	5
Uneven-aged spruce-douglas fir forests	3	–	–	0

^a Number of plots of the class.

^b Total number of specific species ($S > 50\%$).

^c Species also found in $>70\%$ of the plots of the corresponding class.

species, but ubiquitous species were well represented at Rognac (Fig. 3). The profile of habitat preferences at Rurbusch was similar to that in UB forests (Fig. 2d). The best-represented forest stenotopic species in managed forests (*Abax ovalis*, *Carabus auronitens*, *Cychrus attenuatus*, *Carabus coriaceus* and *Molops piceus*) were more frequently found in UB forests than elsewhere.

4. Discussion

4.1. Clear-cutting creates complex conservation effects

The carabid communities of medium and large clear-cuttings (stage 1) showed high conservation values, compared to later stages of the silvicultural cycle. This

was mostly due to high species richness – as recorded by other authors (Niemelä et al., 1993; Ings and Hartley, 1999; Heliölä et al., 2001; Magura et al., 2001) – and to the presence of some rare species and species decreasing at the regional level. This also fits with the results of Butterfield et al. (1995), who observed three times as many rare species in clear-cuttings as in uncut stands. Colonisation of clear-felled sites by open habitat species is a key process enhancing carabid species richness in forests at the landscape level (Baguette and Gérard, 1993). Our results thus confirm the importance of including clear-cuttings in managed forested mosaics for invertebrate conservation.

In afforested extensive meadows, there must be a continuity of clear-cuttings in space and time to maintain biodiversity (Butterfield et al., 1995; Ings and

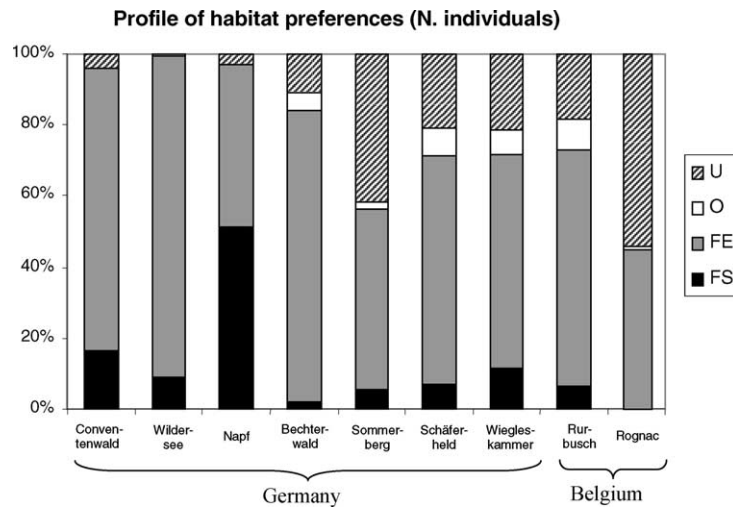


Fig. 3. Profile of habitat preferences of the Carabidae caught in beech- and oak-dominated German and Belgian unmanaged stands. Habitat preferences: U, ubiquitous species; O, open-habitat species; FE, eurytopic forest species; FS, stenotopic forest species.

Hartley, 1999). However, clear-cuttings are temporary open habitats (maximum 10–15 years) and even-aged systems force the populations of open-habitat species to move periodically from one place to another. Some sensitive species will probably never be able to adapt their dynamics to these rapid changes (Butterfield et al., 1995; Gourov et al., 1999). It is therefore likely that clear-cuttings cannot adequately replace extensive meadows.

On the other hand, most typical forest dwellers are large brachypteran species (Dufrêne and Baguette, 1989), which have low colonising capacities (Thiele, 1977), are sensitive to forest fragmentation (De Vries, 1992) and appear to be more subjected to extinction than small species (Pimm et al., 1988). Since clear-cutting can act as a fragmentation factor, it can create risks of extinctions for typical forest species. Moreover, these populations can suffer from the competition of eurytopic open-habitat species, which can remain for more than 20 years in the clear-felled sites (Niemelä et al., 1993). The initial forest community often recovers very slowly after a clear-cut and some typical forest species never come back (Elek et al., 2001). Hence, clear-cutting may lead to a loss of typical forest species at the landscape scale.

The debate concerning the place of open spaces in forests has clear management implications (Svenning, 2002). Starting from extensive meadows, afforestation brings new species, but restricts the original fauna, while starting from forested lands, clear-cutting also brings new species, but can greatly disturb typical forest ones. Our analyses show that small clear-cuttings (0.04–0.20 ha) can also play an important role in maintaining the carabid species richness of forests.

Like Baguette and Gérard (1993), we observed a considerable variation of species profiles in clear-cuttings. In our data, a negative relationship between

species richness and distance to the nearest agricultural habitat in large clear-cuttings ($r = -0.51$, $P < 0.01$) suggests a role of nearby crops and meadows as source habitats in the process of colonisation of clear-cuttings by open-habitat species. Indeed, macropterous, which are often colonising species, were abundant in clear-cuttings of even-aged systems (Fig. 1c). However, Fig. 1d shows that species characterised by very different life histories can coexist in large clear-cuttings. According to Bongers (1990), the communities of clear-cuts are transitory and unstable, far from the “mature” stage (Balent, 1991).

Furthermore, uneven-aged forests are relatively closed systems where the diversity appears to be limited by competitive exclusion: open-habitat species are rare in these forests, which can be explained by the fact that small clear-cuttings are rapidly re-colonised by competitive species inhabiting the forest.

4.2. Effect of tree species composition on conservation value

The impact of tree-species composition has been suggested by several authors (Fahy and Gormally, 1988; Sustek, 1984; Elek et al., 2001; Jukes et al., 2001). A general consensus is emerging concerning the low species richness of medium-aged spruce stands (Day and Carthy, 1988; Butterfield and Malvido, 1992; Niemelä and Halme, 1992; Baguette and Gérard, 1993; Jukes et al., 2001). In these habitats, carabid communities are generally dominated by a few tolerant species such as *Abax ater*, which can constitute up to 85% of the total abundance (Jukes et al., 2001). As we showed, ubiquitous species are highly represented in even-aged conifer forests. Moreover, species abundant in these habitats have been shown to be more generalist and increasing in

Table 7

Mean number of individuals caught per pitfall for each carabid species by groups of habitat types, and comparison between communities of managed and unmanaged stands

Number of pitfalls Number of catching month Managed AND unman. stands	Managed stands (silvicultural system – stage)								Unmanaged stands				
	54 7 E-1	18 7 G-1	36 7 EB2-3	48 7 EC2-3	42 7 EO2-3	36 7 GM2-3	90 7 UB1-3	54 7 UC1-3	18 7 RO	50 8 RU	29 14 LF	30 14 SC	29/30 14 U > 2E
<i>Abax ater</i> Villers	10.93	3.33	45.89	24.63	27.24	21.94	36.93	33.30	++	+	++	+	
<i>Abax ovalis</i> Duftschmid	0.02		1.36			0.53	5.26			++	+	+	
<i>Abax parallelus</i> Duftschmid	2.13		0.19	0.06	0.81		0.04			+	+	+	
<i>Agonum assimile</i> Paykull	0.02			0.52	0.02	0.03			+	+	+	+	+
<i>Agonum fuliginosum</i> Panzer	0.02										+		
<i>Amara aenea</i> De Geer		0.06								+	+		
<i>Amara convexior</i> Stephens	0.04											+	+
<i>Amara familiaris</i> Duftschmid	0.02										+	+	+
<i>Amara lunicollis</i> Schiodte	1.28	0.28			0.07	0.03	0.02			+			
<i>Amara ovata</i> F.	0.02	0.06			0.05			0.04			+	+	
<i>Amara plebeja</i> Gyllenhal	0.07											+	+
<i>Amara similata</i> Gyllenhal		0.06										+	+
<i>Anisodactylus binotatus</i> F.	0.37	0.06								+		+	
<i>Badister bullatus</i> Schrank	0.04				0.02	0.03						+	
<i>Bembidion lampros</i> Herbst	5.56	1.06			0.05	0.03	0.31	0.07	+	+	+	+	+
<i>Bembidion mannerheimi</i> Sahlberg	0.19											+	+
<i>Bradycellus harpalinus</i> Serville	0.50						0.01	0.02			+	+	
<i>Calosoma inquisitor</i> L.					0.26		0.01					+	
<i>Carabus arvensis</i> Herbst	2.72	0.17		1.17	0.31		0.79	0.04			+	+	+
<i>Carabus auronitens</i> F.	0.65		0.08	0.50	0.69		0.27			+	++	+	
<i>Carabus cancellatus</i> Illiger	0.02				0.19							+	
<i>Carabus coriaceus</i> L.	1.59	4.44	1.06	1.52	1.26	2.61	0.20	0.48		+	++	+	
<i>Carabus monilis</i> F.	0.04	0.28		0.02		0.14	0.01	0.02				+	
<i>Carabus nemoralis</i> O.F. Müller	0.59	0.44	0.19	1.77	2.45	0.67	0.18	0.35	+	+	+	+	
<i>Carabus problematicus</i> Herbst	2.72	2.67	13.42	51.92	35.79	22.17	25.72	19.54		+	++	+	
<i>Carabus violaceus</i> F.	0.78	2.22	1.89	0.88	0.19	1.61	0.84	1.09		+	+		
<i>Cychrus attenuatus</i> F.		0.44	2.33	0.33	0.24	2.06	8.11	1.15			++		
<i>Cychrus caraboides</i> L.	0.20	0.06	0.06	0.02	0.02		0.01	0.06			+	+	+
<i>Harpalus latus</i> L.	0.70	0.17			0.02	0.06	0.26			+	+	+	+
<i>Leistus rufomarginatus</i> Duftsch.							0.01		+				
<i>Loricera pilicornis</i> F.		0.06		0.02	0.02		0.03	0.02	+	+	+	+	+
<i>Molops piceus</i> Panzer	0.02	0.11				0.06	0.13				++	+	
<i>Nebria brevicollis</i> F.	0.13		0.08	0.29	0.55	0.17	0.09	0.13	++	+	+	+	
<i>Notiophilus biguttatus</i> F.	0.02	0.06	0.03	0.58	0.02	0.08	0.01	0.24		+	+	+	
<i>Notiophilus palustris</i> Duftschmid	0.19											+	
<i>Pterostichus angustatus</i> Duftsch.	0.13					0.03				+			
<i>Pterostichus cristatus</i> Dufour	0.04		0.06	0.15			0.08		++		++		
<i>Pterostichus cupreus</i> L.	0.46	0.06			0.10		0.03					+	
<i>Pterostichus madidus</i> F.	5.48	0.89	3.81	3.94	6.00	0.89	0.67	0.20	++	+	+	+	
<i>Pterostichus melanarius</i> Illiger	0.07	0.11			0.05		0.03	0.02	+		+	+	+
<i>Pterostichus niger</i> Schaller	2.04	5.72	0.28	2.88	3.40	1.00	1.29	0.93		+	+	+	+
<i>Pterostichus oblongopunctatus</i> F.	6.44	5.94	8.11	9.75	43.07	7.28	24.98	7.81	++	+	++	+	
<i>Pterostichus rhaeticus</i> Heer	0.06	0.11					0.03				+	+	+

Table 7 (continued)

	Managed stands (silvicultural system – stage)								Unmanaged stands				
	54	18	36	48	42	36	90	54	18	50	29	30	29/30
Number of pitfalls	7	7	7	7	7	7	7	7	7	7	8	14	14
Number of catching month	E-1	G-1	EB2-3	EC2-3	EO2-3	GM2-3	UB1-3	UC1-3	RO	RU	LF	SC	U > 2E
Managed AND unman. stands													
<i>Pterostichus strenuus</i> Panzer	0.39	0.33					0.02			+	+	+	
<i>Pterostichus versicolor</i> Sturm	22.15	0.61	0.06	0.02	0.05	0.03	0.41	0.02	+		+		
<i>Stomis pumicatus</i> Panzer	0.02											+	
<i>Synuchus nivalis</i> Panzer							0.08				+	+	
<i>Trechus obtusus</i> Erichson	1.43	0.06	0.06	0.58			0.44		+		+		
<i>Trechus secalis</i> Paykull	4.44	1.39	0.19	0.25	0.07	0.17	0.12	0.20		+			
<i>Trichotichnus laevicollis</i> Duftsch.	0.31		0.03		0.21	0.17	0.21		+	+	+		+
<i>Trichotichnus nitens</i> Heer			0.03	0.02	0.10	0.03	0.96	0.13	+		++	+	+
Total: 51 species	43	29	21	23	30	24	36	22	15	23	35	39	17
Managed stands only	E-1	G-1	EB2-3	EC2-3	EO2-3	GM2-3	UB1-3	UC1-3					
<i>Agonum muelleri</i> Herbst		0.06			0.02	0.03	0.01						
<i>Agonum sexpunctatum</i>	0.02	0.06											
<i>Amara communis</i> Panzer	5.80	2.39	0.03	0.13	0.02	0.06		0.02					
<i>Bembidion quadrimaculatum</i> L.	0.02						0.01						
<i>Bradycellus ruficollis</i> Stephens	0.26												
<i>Calathus melanocephalus</i> L.	0.15												
<i>Carabus auratus</i> L.	0.11												
<i>Cicindela campestris</i> L.	0.19	0.06					0.02						
<i>Dyschirius globosus</i> Herbst	0.22	0.06	0.03			0.06		0.19					
<i>Harpalus affinis</i> Schrank	0.02	0.06		0.02									
<i>Harpalus quadripunctatus</i> Dejean	0.57	0.78			0.05		0.46						
<i>Leistus piceus</i> Fröhlich	0.06			0.06	0.02		0.02	0.02					
<i>Microlestes minutulus</i> Goeze	0.06												
<i>Pterostichus vernalis</i> Panzer	0.15				0.02			0.02					
Total: 14 species	13	7	2	3	5	3	5	4					
Unmanaged stands only	Ecology of the species			Regional status			RO	RU	LF	SC	U > 2E		
<i>Abax carinatus</i> Duftschmid	Forests (stenotopic)			B (rare)	Ard	VR*				+	+		
<i>Agonum dorsalis</i> Pontoppidan	Dry meadows and crops			B	Ard	C				+	+		
<i>Asaphidion flavipes</i> L.	Ubiquist			B	Ard	C				+	+		
<i>Badister lacertosus</i> Sturm	Meadows and forests on rich soils			B	–	MR				+	+		
<i>Bembidion deletum</i> Serville	Forests (eurytopic)			B	Ard	VR			+	+	+		
<i>Bembidion stephensi</i> Crotch	Near water – rare			B	Ard	R			+				
<i>Carabus intricatus</i> L.	Forests (stenotopic)			B (rare)	Ard	R*				+			
<i>Carabus silvestris</i> Panzer	Forests (stenotopic)			–	–	–			+				
<i>Diachromus germanus</i> L.	Wet forests and meadows – rare			B	Ard	VR				+			
<i>Dromius fenestratus</i> F.	Forests (stenotopic. tree creeper)			B	Ard	VR*			+		+		
<i>Harpalus rufipes</i> De Geer	Ubiquist			B	Ard	C				+			
<i>Leistus terminatus</i> Hellwig	Forests and meadows (wet micro-hab.)			B	Ard	R			+				
<i>Molops elatus</i> F.	Forests			–	–	–			+		+		

only about 100 years, and the previous silviculture was an intensive coppice-with-standards regime; (2) it is a small patch surrounded by an intensively managed forest on one side, an open field on a second side and a housing estate on a third; (3) the domination of three generalist species (*Abax ater*, *Pterostichus madidus* and *Nebria brevicollis*) possibly creates a competitive environment excluding other species (important precision). The Rognac and Rurbusch cases illustrate the lack of “valuable” unmanaged stands in southern Belgium (Parviainen et al., 2000). The establishment of a network of strictly unmanaged stands in this region could help rare specialised species to spread.

Within all exploited forests, the carabid communities of medium-aged and mature stands did not significantly differ in most aspects; few species were specific to stage 3. This suggests that our stage 3 cannot be considered as ecologically “mature”. Uneven-aged beech forests clearly contained the highest number of species found in the unmanaged stands, and conifer forests the lowest. This can be explained by the higher periodicity and intensity of human perturbations (felling) in conifer forests, but also by the native character of beech itself in Belgium, since integrity of plant and coleopteran communities can be related (Crisp et al., 1998). It points out the conservation value of UB forests.

5. Conclusion

The first conclusion of our study is obviously the fact that carabid species show higher conservation values in large and medium clear-cuttings than in all other types of habitats. However, this statement must be balanced against the fact that: (1) the species assemblages in cleared areas are unstructured and temporary, and (2) large clear-cuttings increase the risk of extinction of typical forest species. The first point is confirmed by the high ecological diversity of species inhabiting the cuttings – with numbers of ubiquitous and opportunist species – and by the high proportion of species with a great ability for dispersal. Nevertheless, large clear-cuttings should be maintained because they can help to conserve the species inhabiting the surrounding open habitats, where they are threatened by intensive agriculture and urbanisation (e.g. *Carabus cancellatus*, the only officially protected carabid species in southern Belgium).

Special attention should be given to the risk of isolating the populations of typical forest species, as these are less resistant to habitat fragmentation than most open-habitat species. The spatial arrangement of the final cuttings should therefore be planned with prudence in time and space. Long production cycles (long rotations) could greatly reduce the risks, since they allow the forest species to increase their presence and competitive

power. But the initial problem should not be forgotten: the best way to preserve the species representative of extensive meadows is to restore their initial habitats, i.e. to practice extensive grazing.

Our study shows that small clear-cuttings (0.04–0.20 ha) also have an interest for conservation, and that uneven-aged silviculture should be promoted. Our results reinforce a well-known ecological rule, namely that habitat heterogeneity is beneficial for regional biodiversity, in space as well as in time. But, as is illustrated here, heterogeneity has to be implemented on all spatial scales.

Concerning the choice of tree species, we show the high ecological importance of oak stands in sub-mountainous European forests for carabids. Conifer stands, which have an undeniable economic importance in Europe, could have higher conservation potential by lengthening the production cycles and applying specific management practices (see Magura et al., 2000).

Finally, it appears that Belgian managed forests have lost a number of forest species, due to long-term human impacts. Thus, an important and urgent task is to find the carabid diversity hotspots in and around southern Belgium, to secure their conservation and to manage the surroundings in the most favourable way in order to allow their populations to survive and to spread.

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