



Impacts of silvicultural practices on the structure of hemi-edaphic macrofauna community

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Summary

This research determined the influence of six conventional forest management systems on litter-dwelling macrofauna. The forests differed in structure (patch size) and tree composition. Pitfall trapping was carried out in a total of 128 managed stands in the Belgian Ardennes in 1999. We measured the biomass (dry weight) of predators (Arachnida, Carabidae, Staphylinidae and Chilopoda), phytophages (Curculionidae, Homoptera and Elateridae) and detritivores (Lumbricidae, Isopoda and Diplopoda) in young, medium-aged and mature stands in each of the six forest management systems.

The major part of the predator biomass consisted of Carabidae in closed-canopy stages and of Arachnida in the regeneration stage. The main phytophagous group trapped was Curculionidae, except in large regenerating stands where Homoptera showed a higher biomass.

With respect to forest succession, we obtained higher detritivore biomass in regenerating stands, especially in large ones, higher phytophage biomass in medium-aged stands and higher predator biomass in mature stands.

In terms of forest composition, the richest stands as far as biomass and abundance were concerned, were oak forests where predators and detritivores were well represented, followed by coniferous and mixed forests (phytophages). Beech forests appeared to shelter the lowest abundance and biomass of litter-dwelling macro-invertebrates. This impoverishment is partly due to the less favourable edaphic conditions, but also to the silvicultural practices in these forests.

When analysing biomass in terms of forest structure, the size of clear-cut patches was one of the most important features distinguishing even-aged and uneven-aged stands.

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Introduction

For centuries, Belgian forests were subjected to intensive management that was aimed principally at wood production (Devillez and Delhaise, 1991). Only in the last few decades, have some ecologists focused on the effect of this type of management on invertebrate communities, studying the impact of tree species composition, canopy structure, canopy density, clear-cutting, burning or fertilising on the forest entomofauna (e.g. Huhta et al., 1967; Blandin et al., 1980; Heliövaara and Väisänen, 1984; Szujewski, 1987; Niemelä et al., 1993; Theenhaus and Schaefer, 1995; Dajoz, 1998; Jukes et al., 2001). However, studies of this kind were usually restricted to one or some taxonomic groups (and not necessarily litter-dwelling ones) and did not explore the variables characterising forest structure, main tree composition and their landscape pattern. Moreover, they rarely dealt with the ecological structure of the hemi-edaphic macrofauna, which requires quantification of biomass instead of abundance.

The development of the soil food web during the build-up (aggradation) phase of the forest remains poorly understood. Few studies have specifically addressed the issue of how communities of higher-level consumers in the soil food web change during succession (Wardle, 2002). Aside from succession, forest structure and composition are likely to influence predators, phytophages and detritivores – the main litter-dwelling macro-invertebrate taxa that these three functional groups represent. The objective of this paper is to partly fill in these gaps by analysing the ecological structure of hemi-edaphic macro-invertebrate communities using biomass data in three successional stages of forests that differ in structure and composition.

Materials and methods

Study region, sampling design and selection of plots

The study (du Bus de Warnaffe, 2002) took place in the natural region of the Belgian Ardennes (about 5000 km²), situated between the cities of Namur and Luxembourg. The Ardennes are mostly composed of pastures and woodlands, partially transformed into commercial conifer stands during the last 150 years (Devillez and Delhaise, 1991). This region is characterised by a humid sub-montane climate, a hilly relief and loamy acidic soils.

The plots were chosen in order to minimise the variation of climate and soil, and to represent three categories of management variables: the structure of the forest, the composition of the canopy and the stage reached in the silvicultural cycle. The altitude ranged from 320 to 560 m, the mean annual rainfall from 1050 to 1200 mm year⁻¹ and the mean annual temperatures from 6.9 to 7.8 °C (Weissen et al., 1994). All the study plots were on flat or very slightly sloping ground of acidic brown and moderately dry soils (*Dystric cambisol*: FAO, 1990), which were very similar in terms of water and nutrient availability (Table 2). All plots have been maintained under forest for at least 150 years. Plots were all situated in large tracts of forests, at least 100 m apart, and at least 100 m from the nearest field or meadow.

Forest structure, as determined by the mean size of patches (homogeneous stand) in the forest, was evaluated by Geographical Information System (GIS Star-Carto) using aerial photographs. Three classes were distinguished: even-aged (E) where the previous harvest was a large clear-cut (>2 ha), group (G) where the harvest left a medium-sized clear-cuts (0.2–0.5 ha), and uneven-aged (U) where small small clear-cuts (<0.2 ha) were made. According to the terminology of landscape ecology, structure types E, G and U create coarse to fine grains of heterogeneity (Kotliar and Wiens, 1990; Hansson, 1992).

Forest composition classes were defined by the cover of the tree species on 0.04 ha: Class B indicated that more than 75% of the area was covered by beech (*Fagus sylvatica* L.), Class O more than 75% of the area was covered by oaks (*Quercus petraea* (Mattme.) Liebl. and *Quercus robur* L.), Class C more than 75% of the area was covered by spruce and Douglas fir (*Picea abies* (L.) Karst and *Pseudotsuga menziesii* (Mirb.) Franco) or Class M, which referred to a mixture of all species except oak.

Three stages were defined for each combination of structure and composition: regenerating stand (stage 1: trees aged 3–10 years), medium-aged stand (stage 2: trees aged 20–40 years for conifer stands and 30–60 years for beech and oak stands), and mature stand (stage 3: trees aged 50–80 years for conifer stands and 80–140 years for beech and oak stands).

The 18 classes defined by combining structure, composition and stage were called habitat types. In all, 128 plots were selected. The number of plots by class is given in Table 1 and the major features of the plots in the habitat types in Table 2.

Table 1. Number of plots by habitat type

Structure Composition		Even-aged				Uneven-aged		Total
		Conifer EC	Beech EB	Oak EO	Mix GM	Conifer UC	Beech UB	
Silvicultural system	Stage 1	8	6	6	6	5	10	41
	Stage 2	8	6	6	6	7	10	43
	Stage 3	8	6	8	6	6	10	44
Total number of plots		24	18	20	18	18	30	128

See Fig. 1 for codes.

Table 2. Range of the major characteristics of the plots in each habitat type (see Fig. 1 for codes)

Habitat type	Tree species (>75%)	Altitude (m)	pH _{H₂O} ^a (5 cm)	Drainage ^b (a–i)	Mean dbh ^c (cm)	Basal area ^c (m ² ha ⁻¹)	CCS ^d (ha)
EC-1	PA	380–520	4.1–4.7	b	2–7	1–7	4–12
EC-2	PA, PM	320–490	4.2–4.4	b	20–27	34–41	–
EC-3	PA, PM	320–520	3.8–4.1	b	43–50	47–53	–
EB-1	FS	410–540	4.1–4.5	b (c)	2–6	1–5	3–6
EB-2	FS	380–540	3.8–4.4	b	28–44	21–31	–
EB-3	FS	380–460	3.8–4.3	b	43–59	22–28	–
EO-1	QP, QR	320–390	4.2–4.5	b (c)	2–9	2–12	2–5
EO-2	QP, QR	320–400	4.3–4.6	b-c	32–38	20–24	–
EO-3	QP, QR	320–390	4.2–4.8	b (c)	39–44	19–25	–
GM-1	PA, PM, FS	390–560	3.8–4.2	b (c)	1–6	6–14	0.10–0.40
GM-2	PA, PM, FS	390–560	3.8–4.2	b	20–37	21–44	–
GM-3	PA, PM, FS	390–560	3.8–4.2	b	27–50	23–44	–
UC-1	PA, PM	420–560	3.8–4.2	b (c)	2–8	18–27	0.02–0.15
UC-2	PA, PM	420–560	3.6–4.2	b	22–36	32–40	–
UC-3	PA, PM	420–560	3.8–4.2	b	41–52	31–42	–
UB-1	FS (+QP/ QR)	410–500	4.0–4.3	b	1–8	11–20	0.03–0.25
UB-2	FS	350–500	3.8–4.3	b	23–33	17–28	–
UB-3	FS (+QP/ QR)	350–500	3.8–4.2	b	34–52	21–29	–

Tree species (>75% in cover): PA = *Picea abies*; PM = *Pseudotsuga menziesii*; FS = *Fagus sylvatica*; QP = *Quercus petraea*; QR = *Quercus robur*.

^apH_{H₂O} was measured at 5 cm below litter.

^bDrainage = water availability, according to the classification of Weissen et al. (1994), an alphabetic scale ranging from “a” (very dry) to “i” (very moist).

^cMean dbh (diameter at breast height) and basal area of trees were measured on 0.20 ha.

^dCCS = clear-cut size in stage 1.

Arthropod data

We used 8.5 cm diameter × 17 cm deep pitfall traps with 5% formaldehyde to collect ground-dwelling arthropods (Dufrêne, 1988). In each plot, three pitfalls were placed in a triangle of 3 m base (Desender et al., 1999), and emptied monthly

(Heliölä et al., 2001). We sampled the 384 traps for 7 months as recommended by Benest and Cancela da Fonseca (1980) and Döldge (1994), from 10 April to 5 November 1999. Pitfall traps are known to gather valuable information on activity and relative abundance of various groups of ground-dwelling arthropods (Dufrêne, 1988; Branquart et

al., 1995) but inaccurate data on their absolute abundance and density (Sutton, 1972; Branquart et al., 1995; Lang, 2000; Kinnunen et al., 2001).

The trapped taxa were classified according to the main trophic level of the adults. We only considered the major taxonomic groups excluding groups having negligible population density (i.e. Coccinellidae), accidental presence (i.e. some phytophagous taxa trapped during their movements or emergences) or a distribution aggregated around nests (i.e. Formicidae).

For each taxonomic group, we calculated the mean individual biomass by drying 50 randomly selected individuals for 5 days at 67 °C. For most groups, the average individual dry weight obtained was comparable with those obtained in previous studies (Edwards, 1967; Petersen and Luxton, 1982). A notable exception was Arachnida for which the weight obtained was clearly higher than in the literature, probably denoting different species trapped by different trapping methods.

Then, by summing the data over the three traps and over the seven sampling months, we computed 14 parameters of the food web for the 128 plots. The classification of these plots amongst the 18 habitat types allowed us to compute mean values for these 14 parameters: total biomass of predators – which comprised Arachnida (Araneides and Opiliones), Carabidae, Staphylinidae and Chilopoda biomasses; total biomass of phytophages – which comprised Curculionidae, Homoptera and Elateridae biomasses; total biomass of detritivores – which comprised Diplopoda, Isopoda and Lumbricidae biomasses; total biomass (sum of predator, phytophage and detritivore biomasses); and biomass of each taxonomic group. Predator, phytophage and detritivore biomass describe different levels of the litter food-web. Geotrupidae were almost exclusively represented by *Geotrupes stercorosus*. Because of their particular diet (coprophagous), a highly clumped distribution pattern and the fact that the traps appeared to attract them, they were excluded from the analysis.

Quantitative variables

To complete structure, composition and successional stage classes, similar silvicultural variables were measured on surface areas of 0.04 and 0.20 ha in the field and on 3 ha by GIS using 1/10 000 aerial photographs; important environmental variables (factors not controlled by forest managers) were measured on 0.04 ha.

The silvicultural variables measured at these three scales were supposed to be partly redundant

from one scale to another. Therefore, we performed a correlation analysis to suppress the variables of 3 and 0.20 ha scales that were highly correlated with the same variables at 0.04 ha scale ($r^2 > 0.50$; $P < 0.001$). We applied this scheme separately for stage 1 and stages 2+3 because our first results showed sharp biomass differences between stage 1 and 2+3, and small differences between stages 2 and 3. All 0.20 ha scale variables were redundant with the 0.04 ha scale variables, except vertical canopy heterogeneity. None of the 3 ha variables was strongly correlated with the corresponding 0.04 ha ones. Within each spatial scale, no variables were redundant. Hence, in all we had 26 variables for stage 1 and 34 variables for stages 2 and 3 (du Bus de Warnaffe, 2002).

Data analysis

Effects of stand stage, structure and composition

The effects of management variables were tested using Kruskal-Wallis tests (Sokal and Rohlf, 1995) since numerous variables were not normally distributed in the habitat types. The effects of successional stage were tested in all plots and in each of the six combinations of forest structure and composition. The effects of forest structure were tested in all plots, in all plots of each stage, in all beech plots, in all conifer plots, and finally in each stage of beech and of conifer plots. The effects of forest composition were tested in all plots, in all plots of each stage, in all even-aged plots, in all uneven-aged plots, and in each stage of even-aged and of uneven-aged plots. All the tests were performed with the SAS package (2000).

Effects of quantitative variables

Redundancy Analysis (Legendre and Legendre, 1998) showed that structure, composition and stage only explained 9% of the variability of all non-controlled variables. Hence, a linear regression procedure with the SAS package (2000) was used as a complementary approach to relate environmental variables to faunal parameters. Regression analysis was performed separately for conifer stands (stages 2+3), broadleaved stands (stages 2+3) and regenerating stands (stage 1). This separation was done because tree composition and stage strongly influenced the trophic structure (see Results).

Max-R selection procedure (SAS, 2000) was used to determine the variables that best explained the variation of the faunal parameters. A Backward selection (Significance Level to Stay $P = 0.05$) was then performed with the variables of the models, to eliminate the variables that were not significant.

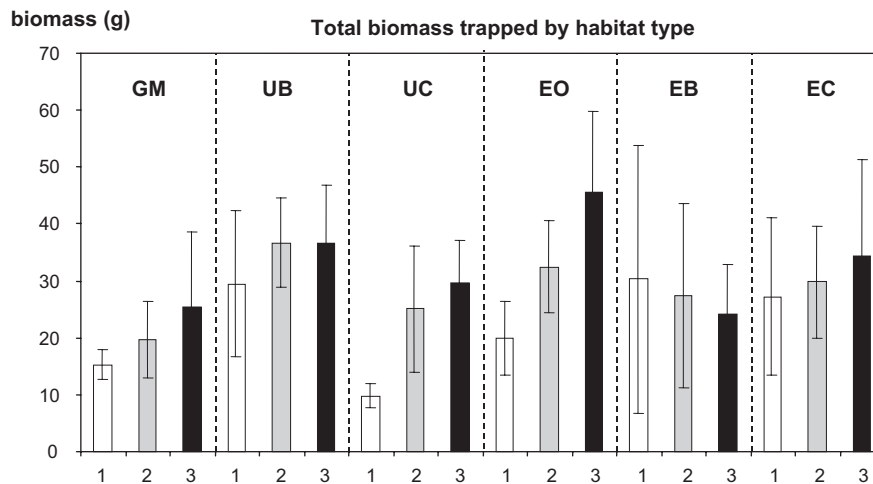


Figure 1. Mean and standard deviation of the total biomass by plot for each habitat type. Combinations of structure (first letter) and composition (second letter) of the stands: group mixed (GM), uneven-aged beech (UB), uneven-aged coniferous (UC), even-aged oak (EO), even-aged beech (EB) and even-aged coniferous (EC). Stages of growth of the stands: 1 = regenerating; 2 = medium-aged and 3 = mature. The number of plots by class are given in Table 1.

Results

Effects of successional stage, structure and composition

Total biomass increased from regenerating to mature stands (Fig. 1), though differences were dependent on structure and composition. Predator biomass constituted 84–98% of the total biomass caught, phytophage <1 to 7% and detritivore 1–13%.

An overview of the mean trophic structure of each habitat type is given by plotting the mean predator, phytophage and detritivore biomass (Fig. 2). Two main groups of habitat types were identified:

- (1) Even-aged and group stage 1, and stages 2 and 3 of even-aged oak, characterised by a high detritivore biomass. This biomass was greater in stage 1 than in stages 2 and 3 ($P < 0.0001$) and greater in oak than in other forest composition types ($P < 0.0001$).
- (2) All other plots.

The second group was divided into:

- (1) Uneven-aged stage 1, characterised by an intermediate detritivore biomass and a low phytophage biomass.
- (2) Stage 2 except even-aged oak, characterised by a low detritivore biomass and a high phytophage biomass.

- (3) Stage 3 except even-aged oak and the mixed group, characterised by a low phytophage biomass and a high biomass of predators.

Within stages 2 and 3, a slight difference appeared between beech and conifer (beech showing a lower detritivore biomass), but no clear difference was observed between even-aged and uneven-aged stands (Fig. 2).

As shown in Table 3, the three management variables (forest structure, composition and stage) had strong effects on the biomass of litter-dwelling macro-invertebrates. Biomass of predators generally increased from stage 1 to 3. The biomass of predators was generally greater in stage 3 (mature), phytophage biomass in stage 2 and detritivore biomass in stage 1. The effect of forest structure was only pronounced in stage 1, with more detritivores in large regenerating stands compared to small ones. A secondary effect was observed in stage 3 of beech forests, with more predators in uneven-aged stands. The impact of composition was significant in stages 2 and 3. Biomass of predators was higher in beech, oak and coniferous forests than in mixed stands ($P = 0.0028$). In even-aged stages 2 and 3, there were significantly more detritivores in oak compared to other composition classes. In uneven-aged stages 1 and 2, there were significantly more predators in beech than in conifer ($P = 0.0013$). In uneven-aged stage 3, there were significantly fewer detritivores in beech than in conifer. So, in terms of stand composition, and with a few exceptions, the biomass of the different trapped

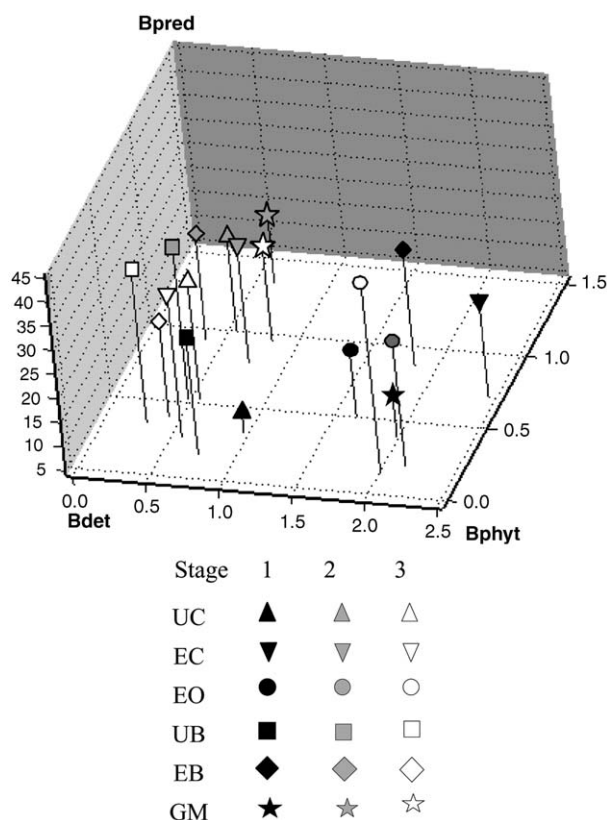


Figure 2. Mean biomass of predators (Bpred), phytophage (Bphyt) and detritivore (Bdet) trapped in each habitat type. Combinations of structure (first letter) and composition (second letter) of the stands: group mixed (GM), uneven-aged beech (UB), uneven-aged coniferous (UC), even-aged oak (EO), even-aged beech (EB) and even-aged coniferous (EC). Stages of growth of the stands: 1 = regenerating; 2 = medium-aged and 3 = mature.

taxa was highest in oak forests, followed by coniferous and mixed forests. Ardennes beech forests appeared to harbour the lowest abundance and biomass of litter-dwelling macro-invertebrates.

Composition of the trophic levels

The majority of predator biomass consisted of Carabidae and Arachnida (mainly *Coelotes* sp., Agelenidae), while Staphylinidae represented only a small percentage of the biomass, and Chilopoda biomass was almost negligible. Carabidae were dominant in biomass in all habitat types. Arachnida biomass was significantly higher in stage 1 than in stages 2 and 3 ($P = 0.0068$), and Carabidae biomass significantly higher in stages 2 and 3 ($P = 0.0001$).

Table 3. Effects of stand structure, composition and stage on the biomass (B) of different trophic levels and of the major hemi-edaphic macro-invertebrate groups of the litter

Tested effect	Structure	Composition	Stage
Total biomass	**	**	***
B predators	**	**	***
B phytophages	ns	**	*
B detritivores	***	****	****
B Arachnida	ns	ns	**
B Carabidae	**	**	***
B Staphylinidae	*	***	ns
B Chilopoda	*	ns	****
B Curculionidae	*	****	****
B Homoptera	***	***	****
B Elateridae	***	****	ns
B Diplopoda	ns	ns	****
B Isopoda	ns	****	ns
B Lumbricidae	****	****	**

Effects are evaluated by the significance levels of Kruskal-Wallis tests (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$; ns, non significant).

The most important phytophagous group trapped was the Curculionidae, except in the even-aged stage 1 where Homoptera showed higher biomass ($P < 0.0001$). In oak stands, the proportion of the three phytophagous taxa seemed well-balanced, notably because of the substantial Elateridae biomass, which was higher than in other stands ($P < 0.0001$).

The Lumbricidae constituted the major part of the detritivore biomass caught, while the Diplopoda was of secondary importance. The biomass of Isopoda was negligible, except in oak stands where it was significantly higher than in other forest compositions ($P < 0.0001$).

Modelling the effects of the quantitative variables

The three models developed for the total biomass explained 79.6–85.6% of the variability. For the biomass of predators, the models explained 71.9–84.7%; for the phytophage biomass, they explained 19.2–80.5%; and for the detritivore biomass, the models explained 59.4–81% (Table 4). The results show that the factors determining the biomass of the different trophic levels greatly differ in conifer, broadleaved and regenerating stands (Table 4).

Table 4. Multiple regression variables for total, predator, phytophage and detritivore biomass in coniferous stands, broadleaved stands and regenerating stands (stage 1)

	Biomass	R^2		Multiple regression variables (%explained >5%; $P < 0.01$)
Coniferous stands of stages 2 and 3 ($N = 35$)	Total	85.6***	+	Mean size of the eco-unit at 3 ha scale***; vertical canopy heterogeneity***; volume of small woody debris***
			–	Altitude*; distance to the nearest crop or meadow***; number of stumps***
	Predator	84.7***	+	Mean size of the eco-unit at 3 ha scale***; vertical canopy heterogeneity***; volume of small woody debris***
			–	Altitude*; distance to the nearest crop or meadow***; number of stumps***
Broadleaved stands of stages 2 and 3 ($N = 52$)	Phytophage	80.5***	+	Percentage of regeneration stage on 3 ha*; altitude***; soil pH**; soil hydric level**; cover of beech*
			–	Vertical canopy heterogeneity*; medium diameter of the trees*
	Detritivore	59.4**	+	Cover of branches on the soil***
			–	Number of stumps**
Regeneration stands (stage 1) ($N = 41$)	Total	79.6***	+	Soil hydric level***; surface of mosses on the barks***; soil compaction***
			–	Cover of conifer on 3 ha**; volume of large woody debris**
	Predator	71.9***	+	Soil hydric level***; surface of mosses on the barks***; soil compaction***
			–	Cover of conifer on 3 ha**
Regeneration stands (stage 1) ($N = 41$)	Phytophage	50.3***	+	Cover of conifer***; number of stumps*
			–	Soil pH**
	Detritivore	81.0***	+	–
			–	Altitude**; percentage of mature stand on 3 ha*; cover of beech*
Regeneration stands (stage 1) ($N = 41$)	Total	81.7***	+	Cover of beech on 3 ha***; size of clear-cutting***
			–	–
	Predator	80.1***	+	Cover of beech on 3 ha***; size of clear-cutting***; cover of mosses on the ground*
			–	–
Regeneration stands (stage 1) ($N = 41$)	Phytophage	19.2***	+	Cover of vascular plants on the ground***
			–	–
	Detritivore	65.4***	+	Percentage of medium-aged stand on 3 ha***; cover of branches on the ground***; size of clear-cutting***
			–	–

Total R -square and P -value for each model are given in the third column (R^2 in %). The sign indicates the positive or negative effect of the variables. Of the total number of variables tested, only variables with significant effects ($P \leq 0.01$) explaining more than 5% in the model are presented. Except when specified, all the variables refer to the 0.04 ha scale (see Table 3).

*** $P \leq 0.0001$; ** $P \leq 0.001$; * $P \leq 0.01$.

Discussion

Methodological implications

Pitfall trapping provides interesting comparisons of the trophic structure of litter-dwelling invertebrate communities. In forests, saprophagous inver-

tebrates are often dominant, while phytophages and predators play a less important role (Dajoz, 1998). Yet predator biomass constitutes the largest part of the total biomass. Whilst pitfall traps are known to gather valuable information on relative abundance of various groups of ground-dwelling arthropods (Dufrêne, 1988), we have to bear in

mind that other groups such as gastropods, caterpillars and other invertebrate larvae may be underestimated by this method.

Wherever environmental variables are intercorrelated, the use of multiple regression methods can create undesirable effects (Palmer, 1993). Even when strong correlations between variables are eliminated, which we did in the present study, other correlations may lead to unstable models or blind selection of variables. The variable selection is based on the correlation of the environmental variable with the response variable and/or a significance test, thus not on the biological relevance of each environmental variable. When two intercorrelated variables are compared, the most important one, biologically speaking, may have lower correlation with the response and may thus be dropped by the programme. However under field conditions, it is impossible to exhaustively describe habitats using only uncorrelated variables. Hence it is very important to take into consideration, as far as possible and in a critical way, redundancies, correlations and the biological meaning of the variables used.

Effects of quantitative variables

Total biomass

Shrub and tree biomass increase with succession providing more and more resources to the ecosystem allowing for an increase in total biomass. Our results support this ecological law of biomass increase during succession as we observed an increase in total biomass from stages 1 to 3 in our study (Odum, 1971; Bormann and Likens, 1979; Wardle, 2002). Moreover, according to Wardle (2002), an increasing ecological role would most likely be played by larger invertebrates in the decomposer food web as the maximal biomass phase of the succession is approached. Unfortunately there are no natural forests in Belgium which could serve as reference stands and where we could have found a "stage 4": ageing and collapsing stages.

Predator biomass

The statement made for total biomass is also true for predator biomass.

Probably because of their thermophily, the biomass of Arachnida was higher in stage 1, increasing their competition with Carabidae at this successional stage. Moreover Carabidae are generally of larger size in forest (stages 2 and 3) than in open habitats (Desender, 1986; Baguette, 1992). These reasons explain the higher biomass of

Carabidae found in stages 2 and 3. Because of their smaller size, it is logical that Staphylinidae biomass reached a lower value in contrast to Carabidae. The beech component on the 3 ha plots contributed to total and predator biomass in stage 1, suggesting exchanges between clearings and the surrounding broadleaved forests.

According to our results clear-cutting has a clearly negative impact on Chilopoda biomass and abundance. A significant decrease was also observed with Staphylinidae. In the literature, however, there is no general agreement about the effect of clear-cutting. Some authors have found decreases while others have observed increases after clear-cutting (Huhta et al., 1967; Theenhaus and Schaefer, 1995). By contrast, the effect of clear-cutting on Carabidae is well studied. Clear-cutting has a definitive impact on Carabidae, depending on species, notably by the replacement of the big forest species by the usually smaller eurytopic open-field species in clearings (Niemela et al., 1993; du Bus de Warnaffe and Lebrun, 2004; Richard et al., 2004).

Centipede biomass per surface unit in forest is generally greater than that of any other major taxa of invertebrate predators (mites, spiders, beetles) (Burgess and Raw, 1967; Edwards et al., 1970; Blandin et al., 1980). In terms of biomass, centipedes would thus constitute a very important component of the predatory fauna in forests (Wignarajah and Phillipson, 1977; Theenhaus and Schaefer, 1995). However in our study, the mean biomass and abundance of Chilopoda were always lower than those of Carabidae, Staphylinidae or Arachnida. Acidic conditions, such as found in the present study, are unfavourable to this group. In addition Chilopoda, and more generally Myriapoda, are highly sensitive to disturbances in the litter (removal of dead wood providing microhabitats and hunting areas, clear-cutting, soils destroyed and compacted by forest machinery), and recolonise the disturbed sites very slowly (Kime, pers. communication).

The three models developed in the current study bring to the fore a variety of influential variables such as the negative effect of altitude on total and predator biomass. The latter is quite logical considering that conditions become increasingly harsher with elevation.

Depending on stand density, the vertical canopy heterogeneity in coniferous stands would allow more light and rain to reach the litter, which would stimulate the litter-dwelling populations. Small woody debris adds interesting microhabitats (hunting grounds, overwintering shelters) to litter that is usually covered by a thick dense needle layer in

conifer stands (Scheu et al., 2003). This needle layer is known to provide little shelter for many of the larger non-burrowing arthropods like Carabidae and Staphylinidae which are generally more abundant in the litter of broadleaved forests (Wallwork, 1976; Dajoz, 1998; Scheu et al., 2003). Our results confirm this statement except for the Staphylinidae whose biomass was the lowest in beech forests.

Detritivore biomass

In the Ardennes, brown soils, the poor quality of the parent material, as well as the usual Ah layer acidic conditions, hinder the settlement of anecic lumbricids (Branquart et al., 1995). This statement is probably also true for other groups known to be negatively influenced by acidity.

Beech and altitude have negative effects on detritivores due to a combination of factors. Firstly, in the Ardennes, beech forests are usually pure because of the poor soil fertility but also because of beech's competitiveness (sciophilous species). Secondly, their density is frequently high and thirdly, beech leaves are highly unpalatable for detritivores because their C/N ratio is very high (Lavelle and Spain, 2001).

By contrast the heliophilous nature of oaks induces a relatively open canopy allowing the development of a mixed forest with a well-developed undergrowth (with *Carpinus* sp., *Acer* sp., *Rubus* sp.) to develop. So whilst the oak litter is also relatively unpalatable, the mixing with other species provides highly palatable litter in comparison with pure beech litter. Consequently, the former litter conditions are highly beneficial for Diplopoda, Isopoda and Lumbricidae. Moreover these groups are negatively affected by soil acidity, which was lowest in oak stands ($P < 0.05$).

The compacted litter generally accumulated under pure, dense spruce and Douglas fir forests provides little shelter and usually exacerbates the existing acidic conditions (Schoy et al., 1984; Andre et al., 1994; Scheu et al., 2003). Such conditions are restricting to certain groups such as Lumbricidae, Diplopoda and Isopoda. Their representation in coniferous forest litter would then be limited to a few acid-tolerant species (Wallwork, 1976; Dajoz, 1998).

Bernier and Ponge (1994) studied the evolution of humus type with *Picea abies* forest succession and the parallel evolution of burrowing earthworms. As the spruce stands grow, the canopy progressively closes and the density of earthworms sharply decreases. By the end of the succession, however, the change in humus type allows the regeneration of these forests and an increase in Lumbricidae populations (Bernier and Ponge, 1994). Because

mean Lumbricidae biomass decreased from stage 1 to 3, our data suggest that our Belgian even-aged coniferous stage 3 had not reached the stage of litter improvement with the current silvicultural practices the maintenance of high tree densities and the cutting of trees when they are around 60–70 years old. In both even-aged and uneven-aged coniferous stands in the current study, the mean biomass of Diplopoda and Isopoda decreased from stage 1 to 3, confirming this idea. Stage 1 is characterised by slash debris on the ground (leaves or needles, twigs, branches, etc.). Furthermore, stumps are often left in clear-cuts, providing a certain quantity of dead wood and shelter for detritivorous species, which could explain their substantial biomass in this stage. Moreover, large clear-cuts are rapidly colonised by pioneer species such as *Betula* sp. and *Sorbus aucuparia* providing highly palatable litter for detritivores (Lavelle and Spain, 2001). So, similarities between oak stands and large clear-cuts in terms of detritivore biomass are explained by the similar conditions between the two habitats.

In the spruce forests of Southern Finland, Huhta et al. (1967) found a lower mean density of Lumbricidae in clear-cuts in comparison with control spruce forests. On the contrary we found the highest biomass of this group in large clear-cuts probably because of the richness and abundance of pioneer trees, shrubs and vascular plants that improve the palatability and quality of the litter. The intermediate detritivore biomass of stage 1 of uneven-aged seems logical, since these habitats are intermediate between closed forests and open habitats with respect to light conditions. This explains the strong influence of clear-cut areas.

Phytophage biomass

Results on phytophage biomass must be treated cautiously because of underestimates caused by the trapping method and because litter is not the usual habitat for this trophic level. Phytophagous groups are mainly present in all vegetation strata above the ground, except during their larval stage, their hibernation period, their search for host plants or their emergence from the soil as imagos.

Our results suggest a partial replacement of Curculionidae by Homoptera following clear-cutting which agrees with Theenhaus and Schaefer (1995) who observed a complete breakdown of the Curculionidae population after clear-cutting.

Hereafter, we detail the key variables in the three models developed.

The plant abundance (grasses, flowers, shrubs, seedlings, etc.), favoured by forest clearance,

plays an important role on phytophage biomass in stage 1.

The large Curculionidae species caught (e.g. *Hylobius* sp. linked to coniferous trees) develop on both young and adult stages of spruce and Douglas fir and need stumps to overwinter. For these two reasons they pass from clearings (notably young spruce stages) to stages 2 and 3. And, because the coniferous percentage influences mainly Curculionidae biomass, this explains the effect of the percentage of regenerating stage on a 3 ha plot on the biomass of phytophages in conifers.

In contrast with their adult diet (phytophagous), the xylophagous and/or predaceous (frequently in dead wood) diet of the Elateridae larvae can explain the positive effect of the number of stumps on phytophage biomass in broadleaved stands. The larvae were found to be more numerous in oak forests compared to beech, conifer and mixed stands where numbers were similar. This group is generally more abundant in the litter of broadleaved forest (Wallwork, 1976; Dajoz, 1998), but was found to predominate in spruce stands rather than beech stands (Scheu et al., 2003).

Effects of stand stage, structure and composition: A synthesis

The three management variables (forest structure, composition and stage) had strong effects on the biomass of litter-dwelling macro-invertebrates.

In the evolution of the trophic structure during forest succession, an increase of total biomass was observed in the present study. At the same time, there was a shift in dominance from detritivores in the regenerating stage (forest clearance favours litter decomposition) to phytophages in the medium-aged stage (intense tree growth) and to predators in the mature stage (high availability of prey in mature forests).

In terms of the impact of forest structure on biomass, the most important difference between even-aged and uneven-aged stands was the size of the clear-cuts (detritivores, Arachnida and Homoptera were favoured by large clearings, while Curculionidae, Carabidae, Staphylinidae and Chilopoda were negatively influenced).

Where forest composition was concerned, the biomass of the different taxa trapped were higher in oak forests, with a few exceptions, followed by coniferous and mixed forests. Beech forests appeared to shelter the lowest abundance and biomass of litter-dwelling macro-invertebrates. In contrast, Scheu et al. (2003) found that the replacement of beech by spruce was associated

with a strong decline in virtually all trophic groups. The impoverishment of the Ardenne beech forest can be explained by the less favourable environmental conditions but also by the intensity of management (closed canopies and pure stands) inducing an almost non-existent understory comparable to pure spruce stands, at least in even-aged structure. The high biomass of litter-dwelling macro-invertebrates observed in coniferous stands vs. beech forests can be explained by the higher quality litter of Douglas fir (less acidic and easier to decompose) compared to that of spruce (acidifying needles) (Rameau et al., 1989; Scheu et al., 2003).

Conclusion

Litter constitutes an ecotone at the crossroad of the soil and the aboveground ecosystems where essential decomposition processes occur, allowing, notably, soil fertility to be maintained. The biomass approach gave us interesting insights into the trophic structure of the litter macrofauna in our study area. This approach would ideally be coupled to a taxonomical approach that provides an understanding of the species within the black boxes of each group.

In order to improve the soil fertility status and humus quality of beech forests, reducing densities, allowing and favouring other indigenous tree species where it is possible, amending the soil where needed, conserving dead trees and dead wood, and lengthening rotations are advisable measures. In coniferous stands, litter quality could be profitably improved by more intensive thinning and mixing with deciduous trees.

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