Does forest management abandonment matter more than habitat characteristics for ground beetles?

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ABSTRACT

Unmanaged forest reserves are designed to preserve or restore typical forest biodiversity, such as forest specialist or dispersal-limited forest species. Yet some species groups might be more dependent on specific habitat features than on forest management per se. We therefore investigated the respective influence of forest management abandonment and habitat characteristics on ground beetles in six French forests comprising both managed and unmanaged areas (85 plots). We hypothesised contrasted responses of carabid species richness depending on ecological and life-history traits (habitat affinity, dispersal ability, diet and moisture affinity). Management abandonment favoured only two ecological groups: forest specialists and openland species. For the other groups, management abandonment was not the main driver. Basal area and humus activity – respectively proxies for canopy closure and food supply – increased total species richness and richness of four ecological groups (forest, wingless, moisture indifferent and carnivorous species). Small scale variables, such as ground vegetation structure, most influenced habitat generalists, winged, hygrophilous and xerophilous species. The effect of forest management abandonment may have been limited either because the reserves we studied have been set aside too recently (15–45 years ago), or because harvesting in the managed forests was relatively extensive (no clearcutting or slash harvesting). We emphasise the importance of taking stand structure into account to plan for biodiversity conservation in managed forests.

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1. Introduction

Reconciling wood production and biodiversity conservation is one of the main objectives of sustainable forest management. Restoration measures, integrated management, and especially management abandonment in strict forest reserves are among the recommendations to prevent biodiversity loss in sustainably-managed forests (Secretariat of the Convention on Biological Diversity, 2009). By restoring natural dynamics, management abandonment aims to ensure the persistence of forest specialist species, which generally have low dispersal ability and high vulnerability towards human-induced environmental changes (Rainio and Niemelä, 2003). In their meta-analysis of European studies, Paillet et al. (2010) showed that forest management has a slightly negative effect on total species richness for different taxa. However, this response varied widely with the taxa considered, and exactly how

reserves can fulfil their conservation role remains a challenging issue. Moreover, the persistence of a species within a reserve depends not only on the suitability of the habitat but also on the quality of the surrounding forest matrix (Hunter, 1999). For both the reserve and the surrounding matrix, understanding which habitat variables matter, and at which scale, is an important issue for conservation.

Although ground beetles have been widely used to assess the impact of habitat change in various environments (Rainio and Niemelä, 2003), most studies analysing the effects of forest management on carabids have shown contrasted results. Depending on the context, forest management can either (i) increase (e.g. Niemela et al., 1993), (ii) decrease (e.g. Magura et al., 2003), (iii) or have no effect on (Magura et al., 2000) the species richness of carabids.

Such results may first indicate that forest management is not the only driver of carabid species richness (du Bus de Warnaffe and Dufrene, 2004). Other multiscale processes may influence carabid species richness patterns in managed and unmanaged stands (Barton et al., 2009; Werner and Raffa, 2000). At a small scale, microclimatic parameters impact carabid communities (Niemela et al., 2007). For example, soil moisture and light intensity usually positively influence biodiversity (Antvogel and Bonn, 2001; Sroka and Finch, 2006), which is also dependent on

structural elements such as leaf litter and deadwood (Pearce et al., 2003; Sroka and Finch, 2006). At the stand scale, in addition to soil conditions (Antvogel and Bonn, 2001), stand characteristics such as dominant tree species, compositional or structural heterogeneity, influence carabid assemblages and diversity (du Bus de Warnaffe and Dufrene, 2004; Janssen et al., 2009; Taboada et al., 2010). In particular, canopy closure seems to be an important structuring factor with higher levels of richness in open- than in closed-canopy stands (Jukes et al., 2001; Vanbergen et al., 2005). As a consequence, confounding effects may appear when comparing managed and unmanaged forests in uncontrolled conditions with respect to stand development stage, exotic tree species or abiotic conditions (Paillet et al., 2010).

Secondly, the type of biodiversity descriptor used in many studies may constrain the revealed patterns. Species richness, the simplest and most intuitive biodiversity index, does not take into account species characteristics (Bengtsson, 1998), such as ecological traits. Yet, these species attributes may determine species responses to environmental variations (Kotze and O'Hara, 2003). For example, forest management can be detrimental to forest specialists and species unable to fly (Sklodowski, 2006) whereas it favours omnivorous species (Latty et al., 2006).

In this context, our paper aims to assess the relative effects of forest management abandonment and habitat characteristics on ground beetles by comparing carabid richness between mature managed and unmanaged forests. (i) We assessed total species richness and species richness for several ecological groups; (ii) we worked on replicated forest sites at a national scale; and (iii) we controlled for site conditions. We sought to answer the following questions: Does management abandonment (between 15 and 45 years) benefit carabid species richness in mature forests? At the plot and trap scales, which habitat characteristics drive carabid species richness, with a particular attention to basal area? Do habitat characteristics explain the observed patterns of carabid species richness better than management abandonment? Are there contrasted responses to the studied variables among species groups?

We expected that unmanaged forests would support more forest specialist, poorly-dispersing, carnivorous and hygrophilous species than managed forests do. Conversely, managed forests would favour more generalist, openland, easily-dispersing, omnivorous and xerophilous species (see den Boer, 1977; Niemela et al., 2007; Purtauf et al., 2005).

2. Materials and methods

2.1. Study sites

Our study was carried out in six French forests (Fig. 1; Table 1), comprising both unmanaged strict reserves and managed areas. No trees in the unmanaged areas had been harvested for at least 15 years (Table 1), whereas the managed areas had been submitted to regular thinning and selective cutting operations. Four of the study sites were located in lowland forests (Auberive; Combe Lavaux; Chizé; Citeaux) and two in mountain forests (Ballons Comtois; Ventron). Within each forest site, plots were selected at random both in reserves and managed areas; this resulted in a 85-plot stratified sampling design (Table 1). The managed plots were selected within a radius of 5 km around the forest reserve boundaries, on similar soil types to those observed in the reserves, and in mature stands composed exclusively of native tree species.

2.2. Beetle sampling

Ground beetles were sampled with pitfall traps in the 85 plots. In each plot, three traps were set 10 m from the centre point along lines radiating out in three different directions (0°, 120° and 240°) to ensure the independence of the traps. Pitfall traps consisted of plastic cups 11-cm deep with an opening of 8.5 cm in diameter. They were set into the ground so that the top of the cup was levelled with the surface. In order to avoid trap flooding, a roof was set up 5 cm above each pitfall trap. Cups were filled with 4 cm of a preservative solution (50% propylene glycol saturated with salt and with a few drops of odourless detergent added). Sampling was carried out monthly over a 3-month period (Table 1). The carabid beetles were identified to species level based on Hurka (1996), Jeannel (1941) and Coulon et al. (2000) and a reference collection. Specimens were stored either in a 70% alcohol solution or in dry collections.

2.3. Species traits

We clustered inventoried species with respect to their habitat affinity, dispersal ability, diet and moisture affinity:

- four categories of habitat affinity were defined based on Desender et al. (2008) and Coulon et al. (2000): openland species, habitat generalists, forest species comprising forest generalists and forest specialists;
- two categories of dispersal abilities were defined based on flight ability. This can be partially inferred from wing type (Kotze et al., 2011). Based on Desender et al. (2008) and Hurka (1996), we distinguished between wingless (poor dispersers) species and species with at least a few winged individuals (including long-winged and di-polymorphic species, easy dispersers);
- three categories of diet were defined based on Ribera et al. (1999), Turin (2000) and Purtauf et al. (2005): carnivorous, mostly phytophagous and omnivorous species;
- three categories of moisture affinity were defined based on Desender et al. (2008) and Coulon et al. (2000): hygrophilous, xerophilous and moisture-indifferent species.

2.4. Environmental variables

2.4.1. Stand variables

Basal area is a simple measurement of stand structure used by foresters. It indicates the amount of woody material and competition among trees. Here, we used basal area as a proxy for canopy closure and light intensity at ground level (Sonohat et al., 2004). At the plot level, total basal area per hectare was quantified in two steps. The diameter of living trees with a Diameter at Breast Height (DBH) of more than 20 cm in lowland forests (resp. DBH > 30 cm in mountain forests) was measured whenever the tree was comprised within a fixed relascopic angle of 2% (resp. 3%). Practically, this means that, in lowlands, any tree with a DBH of 60 cm was sampled at a maximum distance of 30 m from the centre of the plot (resp. 20 m in mountains) and accounted for a basal area of 1 m²/ha (resp. 2.25 m²/ha in mountains). The methods differed between mountain and lowland forests for practical reasons. The diameter of living trees with 7.5 < DBH < 20 cm (resp. 30 cm) was measured within a fixed radius of 10 m (314 m²). In addition, volume of downed deadwood (logs) and standing dead trees (snags) with a diameter >30 cm was measured within a 20 m radius. Snags with a diameter <30 cm were measured within a 10 m radius, and logs with a diameter <30 cm were measured using Line Interect Sampling (LIS, Woodall and Williams, 2005) on a total length of 60 m.

2.4.2. Soil variables

Humus forms were characterised at the plot scale, based on observations at several random locations. Soil organic matter
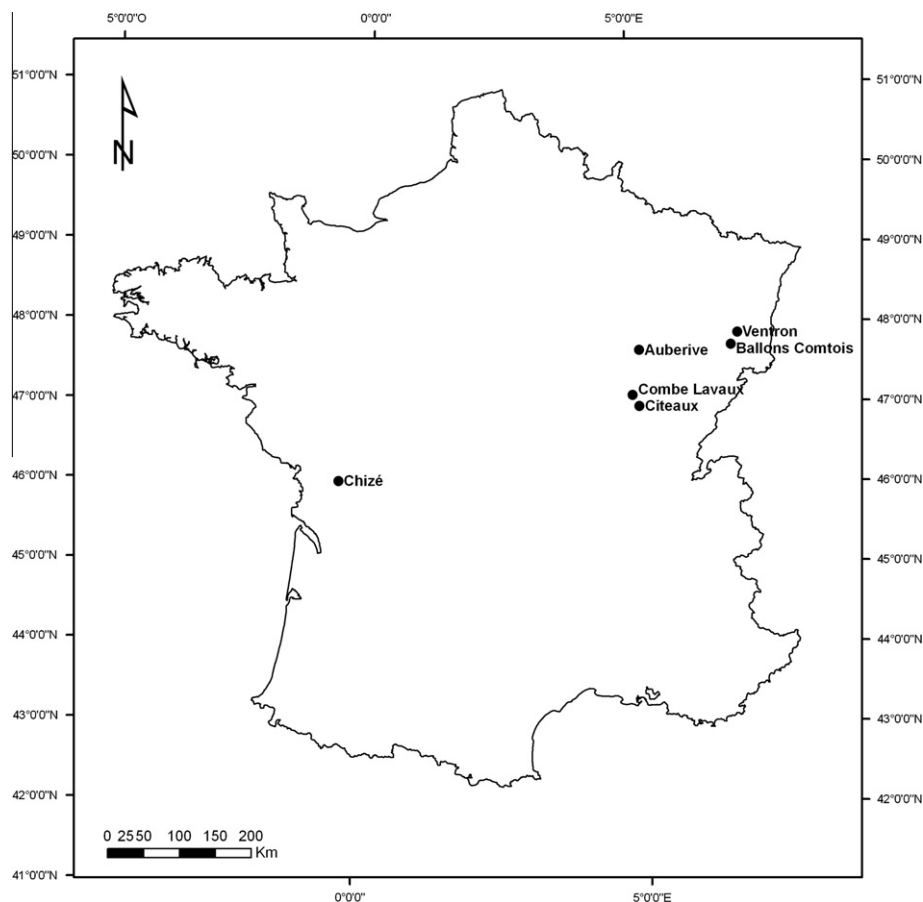
Fig. 1. Location of the six forests studied. Each site includes an unmanaged (strict reserve) and a managed forest area.

Table 1
Study sites characteristics and number of plots in each site.

	Auberive	Chizé	Citeaux	Combe Lavaux	Ventron	Ballons comtois
Site characteristics						
Mean elevation (m)	440	73	200	413	920	1030
Substrate type	Calcareous	Calcareous	Acidic	Calcareous	Acidic	Acidic
Time since abandonment (years)	40	15	45	30	20	>20
Surface area of unmanaged forest reserve (ha)	280	2579	29	300	300	270
Forest type	Mixed beech-oak lowland forest	Mixed beech-oak-hornbeam lowland forest	Oak lowland forest	Mixed beech-oak lowland forest	Mixed beech-fir mountain forest	Mixed beech-fir mountain forest
Management applied in the managed areas	Uneven-aged management	Even-aged management	Even-aged management	Even-aged management	Uneven-aged management	Uneven-aged management
Plot distribution						
Number of plots in managed and unmanaged forests	10 + 10	11 + 11	6 + 6	4 + 4	4 + 4	8 + 7
Sampling period	April-June	May–July	May–July	May–July	June–August	Mid June–mid September
Year	2009	2010	2010	2010	2009	2010

decomposition in the humus layer results from both abiotic and biotic conditions, including stand dynamics (Ponge et al., 2002). Indeed, humus forms (mull, moder, mor) strongly depend on plot topography, vegetation structure and soil biological activities. We adapted the humus index provided by Ponge et al. (2002) to give semi-quantitative values to organic matter accumulation and top-soil biological activity ordered on a scale ranging from 1 to 9 with: 1 (Eumull), 2 (Mesomull), 3 (Oligomull), 4 (Dysmull), 5 (Amphi-mull), 6 (Hemimoder), 7 (Eumoder), 8 (Dysmorder) and 9 (Mor). A value of 1 indicates low acidification and high biological activity and a value of 9, high acidification and low biological activity. In

addition, to characterise differences in abiotic conditions, a pH value was derived from the ground flora community for each plot, using the EcoPlant database (Gégout et al., 2005).

2.4.3. Trap-scale variables

For each ligneous species, saplings (height > 0.5 m and DBH < 7.5 cm) were counted and seedling cover (height < 0.5 m) was estimated within a 1.5 m radius around each pitfall trap. We recorded the presence of a herbaceous layer (cover > 10%) during the trapping season within a radius of 2 m around each pitfall trap. We noted the presence of large living trees (with a DBH larger than

60 cm) within a radius of 10 m around each pitfall trap and coded it as a binary variable in the analyses.

2.5. Statistical analyses

All the analyses were processed with the R software v. 2.5.1 (R Development Core Team, 2007). We compared environmental variables between managed and unmanaged traps with chi-square tests for binary variables and Wilcoxon tests for quantitative variables. We checked the correlations among environmental variables and dropped collinear variables (e.g. altitude was correlated with pH).

Then, we analysed the response of 12 carabid species groups, defined by ecological and life-history traits, to forest management type (managed vs. unmanaged forests) and habitat characteristics. We worked at the trap level in order to assess the respective influence of trap-scale and plot-scale environmental variables on species richness. We therefore used mixed-effect models (i) to take into account potential spatial correlation among traps within a plot and among plots within a site; (ii) to correct for the overestimation of the degrees of freedom induced by pseudoreplication at the trap level (Pinheiro and Bates, 2000).

Two types of response variables were taken into account. First, total species richness: the number of different species observed per trap cumulated over the whole sampling campaign. Second, for each species trait (habitat affinity, dispersal ability, diet and moisture affinity), partial species richness was calculated as the number of species observed for each modality of the trait (observed per trap over the whole trapping campaign). Each response variable was described for 248 observations corresponding to the total number of studied traps (7 pitfall traps were totally destroyed during the sampling campaign).

We considered different types of explanatory variables for species richness: (i) plot-scale variables: management type, basal area – used as a canopy closure proxy-deadwood volume, humus index, soil pH; (ii) trap-scale variables: density of saplings, seedling cover, presence of herbaceous layer and presence of large trees around each trap. As a consequence, for each response variable (total species richness and species richness of ecological groups based on species trait), we compared the effect of management type and habitat variables, by seeking the best explanatory variables among four sets of models built as follows (31 models): (i) simple main environmental effect: one-term model for each potential explanatory variable; (ii) additional effect of basal area or (iii) management type: two-term models systematically including basal area or management type and one other variable; (iv) additional effect of management and basal area: three-term models including management type, basal area and another variable (Table 2). As species richness strongly depends on sampling effort, and to take into account occasional destruction of traps during the sampling campaign, a correction factor was included as a fixed effect in each model (i.e. the logarithm of the number of trapping periods pooled for a given trap).

We used generalised linear mixed models (GLMM) with quasi-Poisson method to account both for over- and under-dispersion. We used the lmer function in the lme4 R package (with the default Laplace approximation for the log-likelihood). By modelling forest site and plot as nested random effects, we introduced hierarchical random effects to take into account the geographical structure of the sampling design. Indeed, we expected plots located within the same forest site (resp. traps within the same plot) to be more similar than plots taken from different forest sites (resp. traps in different plots). We ran models only for response variables with at least 40 non-null values (this meant that phytophagous species richness was not analysed). Following Harrell (2001), we ran multiple regression models only for response variables with a minimum of 100 non-null values to avoid over-parameterisation. For

Table 2
Model sets used to study the link between carabid species richness and management type, habitat structure, trap-scale and soil variables. M = management type (managed vs. unmanaged); BA = total Basal Area per plot.

Model set	Model number	Model composition
One factor model	[0]	Null
	[1]	M
	[2]	BA
	[3]	Sapling density
	[4]	Seedling cover
	[5]	Herbaceous layer
	[6]	Large tree
	[7]	Deadwood
	[8]	pH
	[9]	Humus
Additive basal area	[10]	BA + sapling density
	[11]	BA + seedling cover
	[12]	BA + herbaceous layer
	[13]	BA + large tree
	[14]	BA + deadwood
	[15]	BA + pH
	[16]	BA + humus
Additive management type	[17]	M + sapling density
	[18]	M + seedling cover
	[19]	M + herbaceous layer
	[20]	M + large tree
	[21]	M + deadwood
	[22]	M + pH
	[23]	M + humus
	[24]	M + BA
Additive management type and basal area	[25]	M + BA + sapling density
	[26]	M + BA + seedling cover
	[27]	M + BA + herbaceous layer
	[28]	M + BA + large tree
	[29]	M + BA + deadwood
	[30]	M + BA + pH
	[31]	M + BA + humus

response variables showing between 40 and 100 non-null values, we ran simple regression models. Model selection was based on quasi-Akaike information criterion corrected for small samples (QAICc, Akaike, 1974) and Akaike weights (interpreted as an indication of the relative goodness of fit of the different models Bolker, 2008, p. 284). The model with the lowest QAICc and highest weight was systematically chosen as the best model.

3. Results

3.1. Structure of environmental variables and beetle samples

None of the studied environmental variables differed between managed and unmanaged plots (Table 3). Only seedling cover, pH and deadwood tended to be higher in unmanaged than in managed forests ($p < 0.1$).

Over the three sampling periods, a total of 7916 individuals distributed into 45 carabid species were collected (Appendix A). Forest species (without distinction between generalists and specialists) showed the highest species richness with 25 species (56% of the total species richness), we observed 22 winged species (49% of the total species richness), 24 moisture indifferent species (53% of the total species richness) and 35 carnivorous species (78% of the total species richness, Appendix B).

3.2. Response of carabid beetles

Total species richness best responded to the two-term model including basal area and humus (weight = 25%; Table 4). Total

Table 3
Comparison of the explanatory variables between managed and unmanaged plots. MAN = managed plots; UNM = unmanaged plots. DBH = Diameter at Breast Height. Chi-square tests were used for proportions and Wilcoxon tests for quantitative variables. SD = Standard Deviation.

	MAN	UNM	p-Value
Number of traps	127	121	
Trap scale variables			
Mean number of saplings per trap (SD)	1.9 (3.6)	2.0 (3.8)	0.84
Mean seedling cover (%) per trap (SD)	4.9 (6.3)	6.8 (13.0)	0.10
Proportion of traps with herbaceous layer	49.6	43.8	0.43
Proportion of traps with large tree (DBH > 60 cm)	27.6	31.4	0.60
Plot scale variables			
Mean plot basal area (m²/ha) (SD)	22.5 (6.8)	25.0 (11.7)	0.44
Mean deadwood volume (m³) (SD)	20.9 (24.6)	34.3 (35.5)	0.09
Mean humus index (SD)	2.7 (1.5)	2.8 (1.8)	0.89
Mean pH (SD)	5.9 (0.9)	6.0 (0.9)	0.09

species richness increased with basal area and decreased with humus index (Fig. 2, Table 5).

Habitat generalist species were negatively influenced by seedling cover (weight = 28%; Tables 4 and 5). Openland species richness was higher in unmanaged than in managed forests (weight = 41%). Forest species richness increased with basal area and humus activity (weights = 17%). Active humus forms supported more forest generalist species than less active ones (weight = 19%). Forest specialist species were positively influenced by management abandonment type, but the weight of this model was rather low (weight = 8%). Wingless species richness increased with basal area and decreased with humus index (weight = 20%; Tables 4 and 5). The presence of a herbaceous layer had a positive effect on winged species richness (weight = 31%).

Omnivorous species richness increased with pH (weight = 26%, Tables 4 and 5). Carnivorous species richness increased with basal area and decreased with humus index (weight = 13%).

Xerophilous species richness was negatively influenced by seedling cover (weight = 55%; Tables 4 and 5). Hygrophilous species richness increased with sapling cover (weight = 19%). Moisture-indifferent species richness increased with basal area and decreased with humus index (weight = 13%).

4. Discussion

4.1. Forest management abandonment favours forest specialists and openland species

Forest management abandonment benefitted forest specialists as expected from the literature (Niemela et al., 2007). Indeed, wood harvesting negatively affects some forest specialist species unable to recover from clearcutting during a rotation (Niemela et al., 2007; Sklodowski, 2006; Spence et al., 1996). Either habitat preferences or dispersal limitations may prevent these species from recolonising harvested stands in managed forests (Niemela et al., 1993; Spence et al., 1996). To date, the positive role of management abandonment on forest specialist species has typically been described by comparing unmanaged forests with much younger managed stands or with plantations of exotic tree species (e.g. Magura et al., 2003; Spence et al., 1996). This apparently positive effect may actually result from differences in stand development stages (Koivula et al., 2002) or in tree species composition (Fuller et al., 2008), rather than from management per se. Indeed, when comparing mature managed and unmanaged forests, other studies have not detected any difference in the total species richness or in the abundance of specialist species (Latty et al., 2006; Niemela et al., 1988, 1993; Spence et al., 1996; Werner and Raffa, 2000). Conversely, we showed that forest management may also impact carabid diversity in equivalent mature stages and did benefit forest

specialists. This result supports the fact that the loss of specialist species may be due to human influence (Kotze and O'Hara, 2003).

Surprisingly, forest management abandonment also benefitted the richness of openland species. Indeed, we expected openland species to be more numerous in managed than in unmanaged forests since timber harvesting creates open areas (Niemela et al., 1993). Yet, in mature managed forests, thinning or selective cutting probably does not create enough openings in the canopy to enable colonisation by open-habitat species (Atlegrim et al., 1997; Koivula, 2002; Niemela et al., 2007). This may also imply that the unmanaged forests have a more open – or at least a more heterogeneous – horizontal structure than the mature managed forests (Vanbergen et al., 2005). In turn, species with different ecological requirements, such as openland and forest specialist species may be favoured by heterogeneous light conditions. However, our results should be interpreted cautiously since the openland group only relies on a few species distributed unequally among our study sites. For instance, only one species (*Carabus monilis*) represented most of the occurrences in the openland species group (see Appendix A). Indeed, this species is sometimes classified as habitat generalist (Coulon et al., 2000; Koch, 1989). In this sense, further analyses aiming at specifying species ecological traits appear necessary.

More generally, forest management had no effect on habitat generalist, winged, wingless, omnivorous and carnivorous species in our study. This could be linked to the extensive harvesting methods (i.e. thinning or selective cutting) currently being applied in the managed forests, especially if we compare with more intensive methods such as clearcutting or slash harvesting. Indeed, studies in Fennoscandia have shown that thinning and selective cutting do not particularly affect ground beetle assemblages (Atlegrim et al., 1997; Koivula, 2002). The limited differences we found between managed and unmanaged forests may also stem from the fact that management abandonment was too recent in the reserves we studied (i.e. 15–45 years) to generate distinctive habitat features beneficial to carabids.

4.2. Stand characteristics and soil conditions shape carabid species richness of several ecological groups

4.2.1. Plot- and trap-scale characteristics

At the plot scale, basal area positively influenced total, forest, wingless, moisture-indifferent and carnivorous species richness. Stand basal area is usually interpreted as a canopy-closure gradient (Sonohat et al., 2004). As observed in our results for forest species richness, high basal area usually promotes shade-dependant species (Jukes et al., 2001). However, canopy closure can have opposite effects on carabid species richness depending on the tree species involved, the developmental stage or the stand structure. For

Table 4
Model selection (GLMM with quasi-Poisson method) based on quasi-Akaike Information Criteria corrected for small samples (QAICc) and Akaike weights (W) for total species richness and species richness per group (habitat affinity, dispersal ability, diet, moisture affinity). The model with the highest Akaike weight was systematically chosen. The weights of the selected models are in bold characters. We ran additive models only for response variables with more than 100 non-null values. Model [21] for total species richness did not converge. M = Management type (managed vs. unmanaged); BA = total Basal Area per plot.

| Model number		Total species richness		Habitat generalist		Openland		Forest		Forest generalists		Forest specialists		Wingless		Winged		Carnivorous		Omnivorous		Hygrophilous		Xerophilous		Moisture indifferent	
		QAICc	W	QAICc	W	QAICc	W	QAICc	W	QAICc	W	QAICc	W	QAICc	W	QAICc	W	QAICc	W	QAICc	W	QAICc	W	QAICc	W	QAICc	W
[0]	Null	225.9	0.04	178.3	0.12	191.5	0.07	210.2	0.05	179.3	0.04	241.8	0.03	214.7	0.04	263.6	0.09	223.2	0.05	211.1	0.04	181.5	0.12	188.3	0.04	205.3	0.05
[1]	M	226.6	0.02	178.0	0.14	**188.0**	**0.41**	212.2	0.02	179.3	0.04	**239.7**	**0.08**	215.8	0.02	264.7	0.05	223.7	0.04	213.0	0.02	180.8	0.17	185.2	0.2	207.4	0.02
[2]	BA	225.2	0.05	180.1	0.05	193.2	0.03	210.0	0.06	181.3	0.02	241.1	0.04	213.7	0.07	265.6	0.03	223.0	0.05	212.6	0.02	183.5	0.04	188.9	0.03	205.0	0.06
[3]	Sapling density	227.9	0.01	180.3	0.04	192.7	0.04	212.2	0.02	180.1	0.02	243.1	0.01	216.7	0.02	264.7	0.05	225.0	0.02	212.0	0.03	**180.5**	**0.19**	190.2	0.02	207.3	0.02
[4]	Seedling cover	226.7	0.02	**176.6**	**0.28**	192.2	0.05	211.0	0.05	181.0	0.02	242.8	0.02	214.5	0.05	265.4	0.04	223.8	0.04	213.2	0.02	183.0	0.06	**183.2**	**0.55**	204.8	0.07
[5]	Herbaceous presence	227.0	0.02	177.9	0.15	189.7	0.18	212.2	0.02	181.1	0.02	243.9	0.01	216.7	0.02	**261.2**	**0.31**	224.1	0.03	213.1	0.02	182.2	0.09	187.6	0.06	207.2	0.02
[6]	Large tree	227.0	0.02	180.4	0.04	193.4	0.03	210.2	0.05	181.4	0.02	241.7	0.03	216.6	0.02	265.5	0.04	224.6	0.02	213.1	0.02	183.4	0.05	190.4	0.02	205.4	0.05
[7]	Deadwood	228.0	0.01	180.3	0.05	191.5	0.07	212.1	0.02	180.9	0.02	253.4	0.00	216.6	0.02	265.1	0.05	225.3	0.02	211.7	0.03	183.3	0.05	190.1	0.02	207.4	0.02
[8]	pH	228.0	0.01	179.4	0.07	191.8	0.06	211.1	0.03	181.4	0.02	243.5	0.02	216.3	0.02	261.6	0.26	224.7	0.02	**207.6**	**0.26**	181.7	0.11	188.0	0.05	206.2	0.03
[9]	Humus	224.4	0.08	179.7	0.06	191.9	0.06	209.4	0.08	**176.4**	**0.19**	243.1	0.01	214.1	0.06	264.1	0.07	222.9	0.06	213.1	0.02	181.4	0.12	190.4	0.02	205.0	0.06
[10]	BA + sapling density	227.3	0.02					212.1	0.02	182.7	0.01	242.5	0.02	215.9	0.02			225.1	0.02	213.3	0.02					207.0	0.02
[11]	BA + seedling cover	226.3	0.03					210.6	0.04	182.9	0.01	242.3	0.02	213.9	0.06			223.9	0.04	214.8	0.01					204.8	0.07
[12]	BA + herbaceous presence	226.0	0.03					211.9	0.02	183.0	0.01	243.1	0.01	215.7	0.03			223.5	0.04	214.7	0.01					206.8	0.03
[13]	BA + large tree	227.0	0.02					210.8	0.04	183.3	0.01	241.9	0.03	215.9	0.02			224.8	0.02	214.5	0.01					205.9	0.04
[14]	BA + deadwood	227.1	0.02					211.3	0.03	182.5	0.01	243.1	0.02	215.9	0.02			224.6	0.02	213.3	0.01					207.0	0.02
[15]	BA + pH	227.3	0.02					211.2	0.02	183.3	0.01	243.0	0.02	215.7	0.07			224.8	0.02	208.1	0.2					206.2	0.03
[16]	BA + humus	**222.0**	**0.25**					**207.9**	**0.17**	177.9	0.09	241.3	0.04	**211.6**	**0.2**			**221.2**	**0.14**	214.6	0.01					**203.5**	**0.13**
[17]	M + sapling density	228.7	0.01					214.2	0.01	181.0	0.02	241.0	0.04	217.9	0.01			225.8	0.01	213.9	0.01					209.3	0.01
[18]	M + seedling cover	227.7	0.01					212.6	0.02	180.8	0.02	241.0	0.04	215.9	0.02			224.6	0.03	215.1	0.01					207.0	0.02
[19]	M + herbaceous presence	227.6	0.02					214.1	0.01	181.2	0.02	241.7	0.03	217.8	0.01			224.4	0.03	215.0	0.01					209.3	0.01
[20]	M + large tree	227.9	0.01					212.2	0.02	181.4	0.02	239.9	0.08	217.7	0.01			225.3	0.02	215.0	0.01					207.5	0.02
[21]	M + deadwood	-	-					213.9	0.01	181.3	0.02	241.6	0.03	217.9	0.01			225.5	0.02	213.4	0.01					209.5	0.01
[22]	M + pH	228.7	0.01					213.0	0.01	181.4	0.02	241.2	0.04	217.4	0.01			225.1	0.02	209.4	0.11					208.1	0.01
[23]	M + humus	224.9	0.06					211.3	0.03	176.6	0.18	240.7	0.05	215.1	0.04			223.2	0.05	215.0	0.01					207.0	0.02
[24]	M + BA	226.7	0.02					212.1	0.02	180.9	0.02	240.4	0.06	215.5	0.03			224.3	0.03	214.6	0.01					207.1	0.02
[25]	M + BA + sapling density	228.7	0.01					214.2	0.01	182.4	0.01	241.8	0.03	217.6	0.01			226.4	0.01	215.3	0.01					209.2	0.01
[26]	M + BA + seedling cover	227.9	0.01					212.7	0.02	182.4	0.01	241.9	0.03	215.8	0.02			225.3	0.02	216.7	0.00					207.0	0.02
[27]	M + BA + herbaceous presence	227.4	0.02					214.0	0.01	182.7	0.01	242.3	0.02	217.4	0.01			224.8	0.02	216.7	0.00					208.9	0.01
[28]	M + BA + large tree	228.4	0.01					213.0	0.01	183.0	0.01	241.2	0.04	217.6	0.01			226.2	0.01	216.5	0.00					208.0	0.01
[29]	M + BA + deadwood	228.3	0.01					213.4	0.01	182.7	0.01	241.9	0.03	217.6	0.01			225.5	0.02	215.1	0.01					209.1	0.01
[30]	M + BA + pH	228.8	0.01					213.4	0.01	182.9	0.01	242.1	0.02	217.4	0.01			226.0	0.01	209.9	0.08					208.3	0.01
[31]	M + BA + humus	223.5	0.12					210.0	0.06	177.4	0.11	240.6	0.05	213.4	0.08			222.5	0.07	216.6	0.01					205.7	0.05
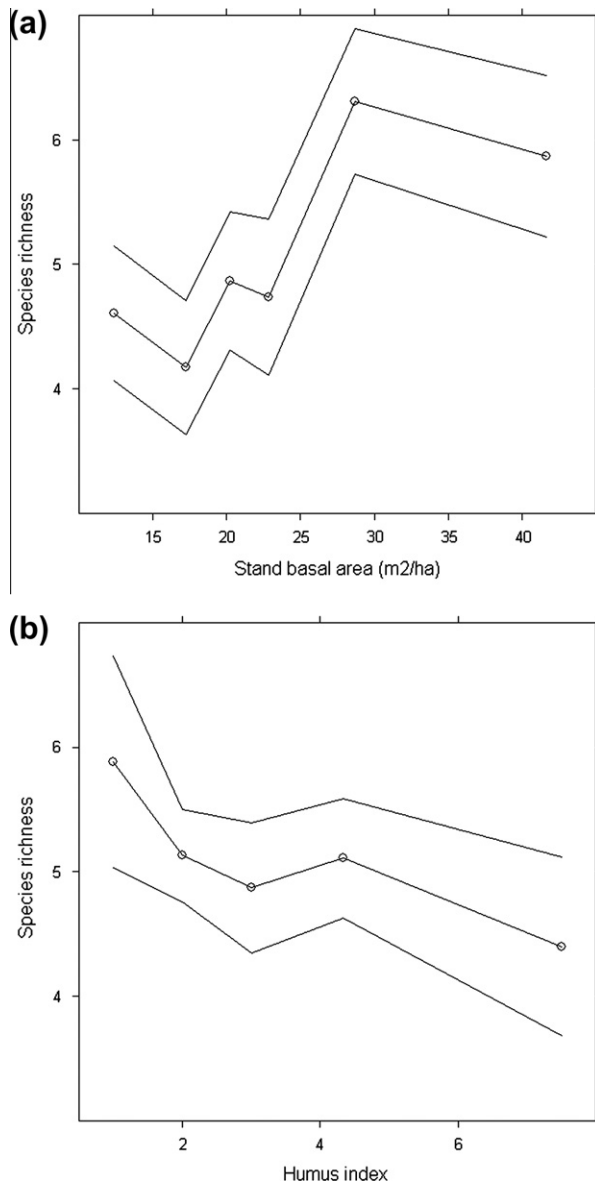
Fig. 2. Relationship between total species richness, and (a) stand basal area or (b) humus index based on raw data. Humus index varies from 1 (Eumull) to 9 (Mor, see text for further details). Each open dot represents the mean value for a minimum of 40 observations (i.e. traps) for basal area (resp. 20 observations for humus index), grouped in ascending order of basal area (resp. humus index). Upper and lower lines represent the 95% confidence intervals (see Harrell (2001) for details on these types of graphical representations).

example, in Canada, the number of ground-dwelling beetle species increases with the basal area of balsam fir and medium-size trees while it tends to decrease with that of black spruce (Janssen et al., 2009). Furthermore, in the mature-stand context of our study, stands with high basal areas and large trees may provide a relatively stable environment suitable for low-dispersal species sensitive to disturbance. High levels of basal area indeed favoured wingless species richness, in accordance with the hypothesis that species with low dispersal power are generally more sensitive to habitat change than well-dispersing species, due to their inability to disperse between suitable habitats (den Boer, 1977).

At the trap-scale, micro-environmental characteristics also influenced carabid assemblages. Vegetation structure is often interpreted in terms of microclimatic conditions (Antvogel and Bonn, 2001; Barton et al., 2009). For example, places where seedlings and saplings develop could correspond to moister situations

favourable to hygrophilous species and detrimental to habitat generalists and xerophilous species. Additionally, winged species are positively influenced by herbaceous layer possibly resulting from canopy gaps. The positive effect of herb cover and the negative effect of shrub cover on total species richness have already been documented (Jukes et al., 2001; Taboada et al., 2010). According to our results, these effects seem to depend on species traits.

4.2.2. Soil pH and humus forms

The composition and diversity of carabid assemblages depend on soil organic matter (Jukes et al., 2001; Taboada et al., 2006) and soil pH (Antvogel and Bonn, 2001), especially on leaf litter cover, depth and quality (Antvogel and Bonn, 2001; Guillemain et al., 1997; Sroka and Finch, 2006). Accordingly, our results are consistent with the previously observed increase of carabid species richness with the decrease of litter thickness (Guillemain et al., 1997), soil organic content (Jukes et al., 2001) and the increase in soil pH (Magura et al., 2003). These relationships are often interpreted in terms of prey availability (Baguette, 1993; Guillemain et al., 1997). Indeed, earthworms, collembola and dipteran larvae, which constitute a diverse potential food resource for carabids, are more abundant in mull humus forms where they play an active role in litter alteration (Ponge et al., 2002; Salmon et al., 2006). On another hand, a higher soil pH can induce a more diverse floristic community (Chytry et al., 2010) and improves the vegetal food supply for omnivorous species, which could explain the observed patterns for this group.

4.3. Convergences in the responses of ecological groups

Total species richness does not take into account the identity and ecological affinity of species nor their response to the studied gradients (Noss, 1990). Therefore, analysing species richness of ecological groups based on habitat affinities (habitat and moisture affinities), life history traits (dispersal power) or functional traits (diet) may prove to be more relevant in determining biodiversity patterns, drivers and potential mechanisms, and consequently may better allow researchers to derive sound conservation orientations (Kotze and O'Hara, 2003). For these reasons, we based our approach on this pluralistic and more mechanistic view of biodiversity response to environmental change. Yet surprisingly, our results indicate rather convergent responses of carabids to environmental change. Four and five out of twelve species groups responded positively to stand basal area and active humus forms, respectively. Moreover, the response of these groups was similar to that of total species richness. This result may be due to the fact that our species pool, restricted to mature forest stands, was mainly composed of forest species (26 out of 45 species) and that the groups considered were partially nested: 17 out of 25 forest species and 18 out of 35 carnivorous species were wingless; 21 out of 25 forest species were moisture-indifferent. Despite these limitations, we still support the use of species ecological attributes in addition to total species richness to better separate convergent from divergent biodiversity responses to environmental changes. In addition, in large-scale bio-geographical studies, using ecological species attributes may help to highlight general patterns that cannot be detected at the species level, since the species pools might be too different among sites to analyse species responses with a sufficient number of occurrences. However, analysing species responses would be a useful complementary approach (Niemela et al., 2007).

5. Conclusions

Forest management abandonment benefited specialist species with contrasted ecological requirements: forest specialist and openland species. The richness of forest, wingless and carnivorous species was mostly affected by specific habitat features and espe-

Table 5
Parameter estimations of the best model for each response variable derived from generalised mixed-effect models with quasi-Poisson method. Basal area and deadwood volume were site-centered for the analysis. SE = Standard error of the estimate.

Response variables	Model	Explanatory variables	Estimate	SE	t-Value
Total richness	[16]	Intercept	1.192	0.091	13.069
		Stand basal area	0.007	0.003	2.557
		Humus index	−0.043	0.016	−2.767
Habitat generalist	[4]	Intercept	−3.002	0.584	−5.140
		Seedling cover	−0.034	0.019	−1.793
Openland	[1]	Intercept	−2.981	0.585	−5.092
		Management type (unmanaged)	0.480	0.169	2.837
Forest	[16]	Intercept	1.078	0.083	13.053
		Stand basal area	0.007	0.003	2.356
		Humus index	−0.036	0.014	−2.496
Forest generalist	[9]	Intercept	0.553	0.082	6.742
		Humus index	−0.041	0.014	−2.891
Forest specialist	[1]	Intercept	0.055	0.155	0.356
		Management type (unmanaged)	0.163	0.067	2.410
Wingless	[16]	Intercept	1.149	0.084	13.758
		Stand basal area	0.007	0.003	2.639
		Humus index	−0.038	0.015	−2.551
Winged	[5]	Intercept	−2.871	0.474	−6.064
		Herbaceous presence	0.514	0.223	2.300
Carnivorous	[16]	Intercept	1.099	0.103	10.683
		Stand basal area	0.007	0.003	2.366
		Humus index	−0.040	0.017	−2.395
Omnivorous	[8]	Intercept	−5.285	1.072	−4.929
		pH	0.575	0.172	3.339
Hygrophilous	[3]	Intercept	−2.529	0.509	−4.971
		Sapling density	0.054	0.026	2.111
Xerophilous	[4]	Intercept	−2.602	0.553	−4.706
		Seedling cover	−0.058	0.025	−2.290
Moisture-indifferent	[16]	Intercept	1.044	0.079	13.209
		Stand basal area	0.007	0.003	2.348
		Humus index	−0.031	0.014	−2.276

cially increased by basal area and active humus forms. Consequently, the most forest-specific and dispersal-limited component of carabids (i.e. forest-specialists and wingless species) require either unmanaged or mature stands with a closed canopy. In terms of conservation, such stands may therefore play an important role both in managed and unmanaged forests. Based on these results, we cannot exclude that a more intensive silviculture which reduces total basal area might erode forest carabid biodiversity. Nevertheless, the relatively low magnitude of these results may be attributed either to the rather extensive style of forest management in our study sites (thinning, selective cutting) or to the relatively recent abandonment of forest management in the reserves (15–45 years).

Appendix A.

Species, abundance and characteristics. Winged species include long-winged and polymorphic species. NA = no information available.

Species	Habitat affinity	Dispersal ability	Diet	Moisture affinity	Abundance
Abax ovalis	Forest specialist	Wingless	Carnivorous	Indifferent	267
Abax parallelepipedus	Forest generalist	Wingless	Carnivorous	Indifferent	3895
Abax parallelus	Forest specialist	Wingless	Carnivorous	Indifferent	290
Amara ovata	Openland	Winged	Mostly phytophagous	Xerophilous	2
Asaphidion sp.	NA	NA	NA	NA	1
Badister meridionalis	Habitat generalist	Winged	Carnivorous	Hygrophilous	1
Badister sp.	NA	NA	NA	NA	1
Calosoma inquisitor	Forest specialist	Winged	Carnivorous	Indifferent	1
Carabus auratus	Habitat generalist	Wingless	Carnivorous	Xerophilous	122
Carabus auronitens	Forest specialist	Wingless	Carnivorous	Indifferent	247
Carabus coriaceus	Forest specialist	Wingless	Carnivorous	Indifferent	18
Carabus granulatus	Habitat generalist	Winged	Carnivorous	Hygrophilous	4
Carabus monilis	Openland	Wingless	Carnivorous	Hygrophilous	545
Carabus nemoralis	Forest generalist	Wingless	Carnivorous	Indifferent	483
Carabus problematicus	Forest generalist	Wingless	Carnivorous	Indifferent	26
Carabus violaceus	Forest generalist	Wingless	Carnivorous	Indifferent	161

Appendix A. (*continued*)

Species	Habitat affinity	Dispersal ability	Diet	Moisture affinity	Abundance
Cychrus attenuatus	Forest specialist	Wingless	Carnivorous	Indifferent	138
Cychrus caraboides	Forest specialist	Wingless	Carnivorous	Indifferent	15
Harpalus atratus	Openland	Winged	Mostly phytophagous	Xerophilous	11
Harpalus latus	Habitat generalist	Winged	Mostly phytophagous	Xerophilous	2
Leistus ferrugineus	Habitat generalist	Winged	Carnivorous	Indifferent	1
Leistus rufomarginatus	Forest generalist	Winged	Carnivorous	Indifferent	9
Limodromus assimilis	Forest generalist	Winged	Carnivorous	Hygrophilous	26
Molops piceus	Forest specialist	Wingless	Carnivorous	Indifferent	33
Nebria brevicollis	Habitat generalist	Winged	Carnivorous	Xerophilous	4
Nebria salina	Openland	Winged	Carnivorous	Xerophilous	2
Nebria sp.	NA	NA	NA	NA	1
Notiophilus biguttatus	Forest generalist	Winged	Carnivorous	Indifferent	2
Notiophilus rufipes	Forest generalist	Winged	Carnivorous	Hygrophilous	4
Notiophilus substriatus	Openland	Winged	Carnivorous	Xerophilous	1
Patrobus atrorufus	Forest specialist	Wingless	Carnivorous	Hygrophilous	8
Poecilus cupreus	Habitat generalist	Winged	Omnivorous	Indifferent	3
Pterostichus aethiops	Forest specialist	Wingless	Carnivorous	Hygrophilous	1
Pterostichus burmeisteri	Forest generalist	Wingless	Carnivorous	Indifferent	180
Pterostichus cristatus	Forest specialist	Wingless	Carnivorous	Indifferent	262
Pterostichus madidus	Forest generalist	Wingless	Omnivorous	Indifferent	964
Pterostichus melanarius	Habitat generalist	Winged	Carnivorous	Xerophilous	22
Pterostichus niger	Forest generalist	Winged	Carnivorous	Indifferent	96
Pterostichus nigrita	Habitat generalist	Winged	Carnivorous	Hygrophilous	2
Pterostichus oblongopunctatus	Forest generalist	Winged	Carnivorous	Indifferent	25
Pterostichus ovoideus	Openland	Wingless	Omnivorous	Indifferent	3
Pterostichus pumilio	Forest generalist	Wingless	Carnivorous	Indifferent	32
Syntomus obscuroguttatus	Openland	Winged	Carnivorous	Xerophilous	1
Trechus obtusus	Habitat generalist	Winged	Carnivorous	Xerophilous	1
Trichotichnus nitens	Forest specialist	Winged	NA	Indifferent	3

Appendix B

Number of individuals and number of species for each species trait. MAN = managed plots; UNM = unmanaged plots. NA = no information available.

		Species richness			Abundance		
		MAN	UNM	Total	MAN	UNM	Total
Habitat affinity	Habitat generalist	6	7	10	58	104	162
	Openland	3	5	7	246	319	565
	Forest	20	25	25	3529	3657	7186
	Forest generalists	11	13	13	2918	2985	5903
	Forest specialists	9	12	12	611	672	1283
	NA	2	1	3	2	1	3
Dispersal	Winged	12	17	22	84	139	223

Appendix B (*continued*)

		Species richness			Abundance		
		MAN	UNM	Total	MAN	UNM	Total
ability	Wingless	17	20	20	3749	3941	7690
	NA	2	1	3	2	1	3
Diet	Carnivorous	25	31	35	3419	3506	6925
	Omnivorous	2	3	3	411	559	970
	Mostly phytophagous	1	2	3	2	13	15
	NA	3	2	4	3	3	6
Moisture affinity	Hygrophilous	4	6	8	261	330	591
	Xerophilous	5	7	10	53	115	168
	Indifferent	20	24	24	3519	3635	7154
	NA	2	1	3	2	1	3
Total		31	38	45	3835	4081	7916

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