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Diversity of ground beetles (Coleoptera, Carabidae): does forest management matter?

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Abstract

Forest management is suspected to negatively impact biodiversity, but this impact varies greatly between taxonomic groups. Although ground beetles are often used to assess the impact of habitat changes, few studies have compared carabid communities between managed and unmanaged forest stands. In this study we compared the diversity of carabids in terms of total species richness and species richness of several ecological groups (trophic groups, canopy-openess affinities, dispersal ability and moisture affinities) within six French forest sites comprising managed and unmanaged areas. We set up 269 pitfall traps distributed across 92 plots. We analysed the effects of management type, stand basal area and microenvironmental variables on carabid diversity. We found that management did not influence carabid total and partial species richness. Yet, diversity was influenced by, depending on the ecological group, stand basal area, humus form, sapling density, seedling cover and abiotic parameters (pH, elevation). Our results suppose that maintenance of landscape heterogeneity is necessary to promote overall ground beetle diversity. Moreover we shown that forest specialist species diversity is positively dependant on stand basal area, special attention should be paid to conserve adult stands in the landscape for the preservation of this specific diversity.

Keywords: basal area, carabid, ecological group, forest management, microenvironment

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Introduction

Reconciling productivity and biodiversity is one of the main challenges in sustainable forest management as defined by the Ministerial Conference on the Protection of Forests in Europe (MCPFE 2003). Therefore, how biodiversity responds to forestry practices is still an important question for both ecologists and foresters (Ehrlich 1996; Simberloff 1999). Forest management can be described as a voluntary exportation process of all or a significant proportion of the woody biomass of a forest area in a short time compared to the duration of a natural forest cycle, with methods that vary in their nature and organisation (Deconchat 1999). According to this definition, forestry practices are especially susceptible to modify disturbance regime, availability of successional stages in the landscape, main tree species, living and dead wood volumes and nutrient cycles in managed stands as compared to unmanaged stands.

Assessing the impact of forest management on biodiversity requires comparing different types of managed forests with protected forests, used as controls stands, in similar abiotic conditions. Unfortunately, such studies are rare, possibly because protected forests represent less than 2% of the forest surface area in Europe (Parviainen et al. 2000). In their meta-analysis of the published European studies, Paillet et al. (2010) showed that forest management has a slightly negative effect on species richness. However, this effect strongly depends on the taxa considered. Whereas vascular plants are favoured by the openings resulting from forest management, other taxa, such as bryophytes, lichens, fungi, saproxylic beetles, but also ground beetles (Coleoptera, Carabidae), are negatively affected by forest management. Moreover, the authors identified a gap in knowledge concerning the European temperate region and the taxa that were negatively affected by forest management: most studies used in this meta-analysis concerned the boreal biome, whereas in temperate forests, investigations on invertebrates, especially carabids, remained rare.

Indeed, although ground beetles are a relevant tool to assess the impact of habitat change (Rainio and Niemela 2003), few studies have compared carabid communities in managed and unmanaged forest stands. Furthermore, these studies showed contrasted results. Depending on the context, forest management can either (i) increase (e.g. Haila et al. 1994; Niemela et al. 1993) (ii) decrease (e.g. Magura et al. 2003; Poole et al. 2003), (iii) or have no effect on (Humphrey et al. 1999; Magura et al. 2000) the species richness of carabids.

Firstly, such contrasted results may indicate that forest management is not the only factor involved in variations in the carabid species richness. Other explanatory variables, possibly at

other spatial scales, may influence carabid species richness patterns in managed and unmanaged stands. Indeed, carabid communities are driven by multi-scale processes (Barton et al. 2009; Sroka and Finch 2006). At a small scale, microclimatic parameters impact carabid communities (Niemela 1997; Werner and Raffa 2000). For example, soil moisture and light intensity are positively correlated with carabid richness (Antvogel and Bonn 2001; Sroka and Finch 2006). Species richness is also dependent on structural elements such as leaf litter and dead wood (Pearce et al. 2004; Poole et al. 2003; Sroka and Finch 2006).

Secondly, the type of biodiversity descriptor used in these studies may constrain the revealed patterns. Species richness, the simplest and the most intuitive biodiversity measurement, does not take into account species characteristics (Bengtsson 1998), such as functional and life-history traits. Yet, these species attributes may determine species responses to environmental variations. For example, logging residues removal in clear-cut may lead to an increase in generalist species and a decrease in forest species (Nitterus et al. 2007).

Thirdly, due to the rarity of unmanaged forests, some studies compared managed and unmanaged forests on a very restricted number of independent sites and in uncontrolled conditions with respect to stand development stage, main tree species, or abiotic conditions, which is susceptible to induce confounding effects (Paillet et al. 2010).

In this context, our paper aims at assessing the effects of forest management on ground beetles by comparing carabid diversity between managed and unmanaged forest stands: (i) in replicated forest sites at a national scale; and (ii) with a control of ecological conditions. This study is a part of a national scale project evaluating the effects of forest management on the diversity of different taxa. We sought to answer the following question: What is the relative influence of forest management, basal area and microenvironment on the diversity of ground beetles?

We hypothesized that unmanaged forests support more carabid species than managed forests. We also expected microenvironmental variables to better explain the species richness patterns than stand-level variables do. Finally, we assumed that ecological groups based on species traits showed contrasted responses to the studied environmental factors.

Materials and methods

Study sites

Our study was carried out in six French forests (Fig. 1; Table 1). Study sites were selected among forests that contained both strict nature reserves and managed forest areas. 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. The managed plots were selected within a radius of 5km around the forest reserve boundaries, on similar soil types than those observed in the reserves, and in stands corresponding to the same stage of development. For example, when the reserves did not include any regenerating stands (resulting from natural disturbance), this stage was excluded from the random selection in managed areas. Finally, only 2 regenerating plots in Chizé and 2 in Auberive were included in the dataset. A total of 92 plots were selected (Table 1).

Beetle sampling

Ground beetles were sampled with pitfall traps. Each plot comprised a set of three traps located at 10m from the center of the plot, in three directions to insure independence of the traps: 0 grades (P1), 133 grades (P2), 267 grades (P3). Pitfall traps consisted of plastic cups with on opening diameter of 8.5 mm and a depth of 11cm. They were set into the ground so that the top of the cup was levelled with the ground surface. In order to avoid trap flooding, a roof was set 5 cm above each pitfall trap. Cups were filled with 4 cm of a preservative solution (50% propylene glycol, saturated in salt and with a few drops of odourless detergent added). Sampling was carried out monthly over a three month period (Table 1). Then carabid beetles were identified to species level using Hurka (1996), Jeannel (1941) and Coulon et al. (2000) and a reference collection. Species were stored either in a 70% alcohol solution or in dry collections.

Species traits

We clustered species with respect to their trophic groups, canopy-openess affinities, dispersal ability and moisture affinities.

Dispersal abilities: carabids show several wing development types that may vary from full, to partial or null development of hind wings (Kotze et al. 2011). As a consequence, some species are able to fly and disperse on long distances whereas others can only walk and disperse on shorter distances. This differential dispersal ability can influence carabid communities assemblages (Verhagen et al. 2008). We used Desender et al. (2008) and Hurka (1996) typologies to distinguish between brachypterous (short-winged) and non-brachypterous species. This latter group included macropterous (large-winged) and di-poly-morphic species (wing types differing between individuals).

Tropic groups : as trophic groups are dependent on specific resources potentially impacted by anthropogenic activities (Purtauf et al. 2005), we divided species into carnivorous, phytophagous and omnivorous species based on literature (Cole et al. 2002; Ribera et al. 1999; Turin 2000).

Canopy-openess affinities: Forest harvesting primarily acts on canopy cover, which affects the ecological requirements of some carabid species (Rainio and Niemela 2003). We relied on Desender et al. (2008) and Koch (1989) to classify the inventoried species into four categories: openland, generalist, forest eurytopic (using several forest types) and forest stenotopic (restricted to a forest type) species.

Moisture affinity: as we expected structural variables to provide different microclimatic conditions, species were classified into hygrophilous, xerophilous and indifferent-to-humidity species. This classification was based on Desender et al. (1995) and Coulon et al. (2000).

Environmental variables

Stand Variables: stand structure and tree species composition were characterised using an existing protocol designed to monitor French forest reserves and adapted in the context of mountains. The diameter of living trees with a Diameter at Breast Height (DBH) of more than 20 cm in lowland forests (resp. DBH > 30cm 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, a tree with a DBH of 60cm was sampled at a maximum distance of 30 m from the centre of the plot (resp. 20m in mountains) and accounted for a basal area of

1m²/ha (resp. 2.25m²/ha in mountains). Basal area was then expressed as the total basal area per hectare at the plot level.

Microenvironmental variables: for each ligneous species, saplings (height > 0,5m and DBH < 7.5cm) were counted within a circle of 1,5m radius around each pitfall trap. Hence we obtained a density of saplings per trap. Within the same circle, cover of seedlings (height < 0.5m) was noted around each trap.

Other microenvironmental variables were investigated within a radius 2m around each pitfall trap, during the trapping season. We recorded the presence of herbaceous layer (bryophytes and forbs); living trees with a DBH >30 cm and dead wood (including windfalls, logs, snags and stumps, with a diameter > 10 cm).

Humus forms were sampled at the plot scale at several random locations to obtain an "average" humus form for each plot. As humus constitutes a living environment for carabids, we also considered it as a microenvironmental variable. Humus represents soil organic-matter decomposition resulting from both abiotic conditions and stand dynamics (Ponge and Chevalier, 2006). Indeed, humus forms (mull, moder, mor) strongly depend on plot topography, vegetation structure and soil biological activities. Soil biological activity per se is under the control of climatic and soil biochemical characteristics. Hence humus provides qualitative information on ecosystem abiotic and biotic properties. Based on this relationship, we adapted the Humus Index provided by Ponge and Chevalier (2006) and Ponge et al. (2002) to give a semi-quantitative value to assess organic matter accumulation and topsoil biological activity. This index is ordered on a scale ranging from 1 (Eumull) to 8 (Mor) with: 1 (Eumull), 2 (Mesomull), 3 (Oligomull), 4 (Dysmull), 5 (Hemimoder), 6 (Eumoder), 7 (Dysmorder) and 8 (Mor). A value of 1 indicates low acidification and high biological activity and a value of 8 means high acidification and low biological activity.

In addition, a pH value was derived from the ground flora community for each plot, using the French Ecoplant database (Gégout et al. 2005).

Statistical analyses

All the analyses were processed with the R software v. 2.5.1 (R Development Core Team 2007). To detect differences among environmental variables between managed and unmanaged stands, we used chi-square tests for binary variables and wilcoxon tests for quantitative variables. Two types of response variables were taken into account. Firstly, total species richness represented the number of different species observed per trap cumulated over

the whole sampling campaign. Secondly, for each species trait (dispersal ability, tropic groups, canopy-openess affinities, moisture affinities), a partial species richness was calculated as the number of species (observed per trap over the whole trapping campaign) observed for each modality of the trait. Each response variable was described on 269 observations corresponding to the total number of studied traps (17 pitfall traps over the three periods have been totally destroyed during the sampling campaign).

Furthermore, we considered different types of explanatory variables for the trap contents: (i) microenvironmental variables corresponding to humus form (coded as humus index) and the presence of living trees, deadwood, herbaceous layer (bryophytes and herbaceous plants), density of saplings, cover of seedlings within a radius of 1.5 or 2m around each trap; (ii) stand-level variables: management type, basal area and (iii) abiotic variables (soil pH and elevation). As a consequence, a set of 19 models that we assumed to be relevant regarding our hypotheses was fitted for each response variable (total species richness and ecological group based on species trait):

[0] Null

[1 - 10] One factor model: Elevation, pH, Humus, Herbaceous layer, Seedling, Sapling, Living wood, Dead wood, Management, Stand basal area

[11] Herbaceous layer + Seedling + Sapling + Living wood + Dead wood

[12] Management + Stand basal area

[13] Management + Herbaceous layer + Seedling + Sapling + Living wood + Dead wood

[14] Management + Humus

[15] Stand basal area + Herbaceous layer + Seedling + Sapling + Living wood + Dead wood

[16] Stand basal area + Humus

[17] Humus + Herbaceous layer + Seedling + Sapling + Living wood + Dead wood

[18] Complete additive: Management + Stand basal area + Humus + Herbaceous layer + Seedling + Sapling + Living wood + Dead wood

We used quasi-Poisson generalized linear mixed models (GLMM) to study the response of carabid species richness to environmental variables. Contrary to the assumptions of the Poisson distribution, mean was not equal to the variance in our dataset, we hence corrected standard errors using the quasi-Poisson method.

To run the models, we used the lmer function in the lme4 R package (with the default Laplace approximation to the log-likelihood). We introduced hierarchical random effects to take into account the geographical structure of the sampling design, based on several plots within the

same forest sites, and several traps within the same plot. Indeed, we expected plots located within the same forest site to be more similar than plots taken from different forest sites. Respectively, we expected traps located in the same plot to be more correlated than traps from different plots. Therefore, a random "plot nested in site" effect was included in the models to take this source of spatial autocorrelation into account. We ran models only for response variables with at least 40 occurrences (hence we excluded richness of phytophagous species). Following Harrell (2001), we ran additive models only for response variables with a minimum of 100 occurrences to avoid overparameterisation. As species richness strongly depends on sampling effort (Gotelli and Colwell 2001), a correction factor was included as a fixed effect in each model, in order to take into account destruction of traps during the sampling campaign. The goodness of fit of statistical models was measured with the quasi-Akaike information criterion corrected for small samples (QAICc, Akaike 1974) and Akaike weights (Bolker et al. 2009). The model with the lowest QAICc and the highest weight was systematically chosen as the best model.

Results

Structure of environmental variables and beetle sample

We found no significant differences of environmental variable between managed and unmanaged (Table 2). Over the three sampling periods, a total of 8802 individuals distributed into 44 carabid species were collected (Appendix 1). The most abundant species groups were woodland eurytopic with 6266 individuals (71% of the total abundance), brachypterous with 8499 individuals (96% of the total abundance), moisture indifferent with 7770 individuals (88% of the total abundance) and carnivorous with 7008 individuals (77% of the total abundance). Woodland stenotopic species showed the highest species richness with 15 species (34% of the total species richness), non-brachypterous species represented 23 species (52% of the total species richness), moisture indifferent species represented 23 species (52% of the total species richness) and carnivorous species represented 37 species (84% of the total species richness, appendix 2).

Total species richness

Total species richness best responded to the additive stand basal area and humus model (Table 3). Total species richness slightly increased with stand basal area and decreased with increasing humus index (Table 4).

Groups' species richness

Regarding carabid canopy-openess affinities, generalist species were mainly influenced by seedling cover (Table 3). An increase in seedling cover reduced generalist species diversity (Table 4). Openland species were mainly and positively influenced by sapling density. For woodland eurytopic species, the best model was the null model. In contrast, woodland stenotopic species diversity was mainly influenced by the additive model including stand basal area and humus index. Stand basal area had a positive effect on specialist woodland species diversity and humus index had a negative effect.

Concerning carabid dispersal ability, brachypterous species diversity was also better explained by the additive model with stand basal area and humus. Trends were the same as previously observed: stand basal area had a positive effect and diversity decreased with

increasing humus index. For non-brachypterous species diversity, the one-factor model humus had the highest weight. Non-brachypterous species richness decreased as humus index increased.

The trophic groups presented different patterns. The best model for omnivorous species diversity was pH. Omnivorous species diversity was positively influenced by pH. For carnivorous species, the best model was the additive stand basal area and humus model. Species diversity responded positively to the stand basal area and negatively to humus index.

The three moisture affinity groups showed diverging responses. The best model for xerophilous species was elevation, hence species richness was slightly higher at low than at high elevations. Hygrophilous species were influenced by the sapling density. Hygrophilous species responded positively to the sapling cover. Moisture-indifferent species richness responded to the additive model involving stand basal areas and humus. Species richness increased with stand basal area and decreased with humus index.

Discussion

No effect of forest management on carabid beetles

Our results did not support the hypothesis that forest management directly determines carabid diversity. However, to our knowledge, our study differs from the previous ones by the fact that the managed and unmanaged stands were comparable in terms of abiotic conditions, tree species pool and stand developmental stage: we worked mostly in mature adult forests. Indeed, studies that obtained effects of forest management on carabid species compared plantations to native forests (Day et al. 1993; Finch 2005; Magura et al. 2003), or analysed carabid species diversity between mature and regenerating sites (Poole et al. 2003). Here, we only tested the effects of forest management on a restricted range of the sylvicultural cycle, which could limit the detection of carabid community response to forest management. Moreover, the managed stands did not differ from the unmanged stands as regards to any of the studied environmental variables.

On another hand, the rapid response of carabids to habitat change (Martikainen et al. 2006) may mask the effects of forest management. Previous studies have shown that, few years after logging, species richness increases due to the colonization by open habitat species and the persistence of few forest generalist species (Work et al. 2010) whereas forest specialists disappear. Then, forest generalists recolonize stands during the tree growth phase. Finally, a few forest specialists may be absent in mature stands due to their incapacity to survive in or recolonize cut-over stands (Niemela et al. 1993; Sklodowski 2006). Such dynamics could limit the detection of carabid diversity differences between managed and unmanaged adult forests.

Stand basal area and microenvironment both matter

We found that both microenvironmental-level and stand-level structure of the habitat influenced the diversity of carabids. Our results showed that stand basal area seemed particularly important for total, woodland stenotopic, brachypterous, moisture indifferent and carnivore species were similarly influenced by basal area and humus form. Indeed, stand basal area is positively correlated with a shading gradient and lead to promote shade-tolerant forest specialist species (Jukes et al. 2001). Moreover, we also showed that diversity of species with a low power of dispersion was higher in mature stands. Species with large bodies and poor

dispersal ability are generally more sensitive to habitat alteration due to their inability to disperse between suitable habitats (Kotze and O'Hara 2003). To some extent, adult stands could provide a relatively stable environment suitable for species with low dispersal ability.

From a microenvironmental point of view, we found that carabid diversity was enhanced by the humus forms showing a high top soil biological activity and a low organic matter accumulation. Carabid beetle diversity usually relies on leaf litter (Magura et al. 2005) which might provide some beneficial microenvironmental conditions, shelter and improve food supply (Koivula et al. 1999). However, humus with high pH support higher densities of collembolan species, centipedes and macrofauna (Salmon et al. 2006). Earthworms, springtails and dipteran larvae play an active role in litter alteration, and constitute an important food resource for carabids. This could explain the beneficial role of humus with high top soil biological activity and a low organic matter accumulation. Indeed, other authors have shown that the influence of soil type on carabid community composition is strong (Walsh et al. 1993).

Other microenvironmental variables influenced carabid diversity in our study: we found that sapling and seedling densities were determinant for openland, hygrophylous and habitat generalist species. Some studies support the hypothesis that vegetation structure provides some beneficial microclimatic conditions for carabid beeltes (Thiele 1977): in our study, the diversity of hygrophilous species was positively correlated by presence of ligneous ground vegetation, which confirms the role of the vegetation in providing favourable microclimatic conditions for some species. We found that sapling density was important for openland species richness. This result reinforce the observed link between gap dynamics in the forest canopy and species turnover, especially the colonization by openland species few years after logging (Koivula and Niemela 2003). Quite surprisingly, habitat generalist diversity tended to be negatively impacted by seedling cover. The effect of ground vegetation on ground beetle has often been stressed in literature and other types of small scale vegetation structure, like herb layer, are also important for ground beetle assemblages (Ings and Hartley 1999). But this effect may rather rely on sampling methods than ecological process. Indeed, ground vegetation around pitfall traps could interfere with carabid movements, thus reducing catches (Greenslade 1964). Our result may be explained by such a sampling effect.

Effect of abiotic factors

Abiotic factors were important for xerophylous and omnivorous species. Studies relating carabid diversity and pH are scarce (Antvogel and Bonn 2001). Diversity of xerophylous species was higher in lowland than in mountain forests, which could simply be linked to the higher rate of precipitations in the mountain areas studied. This kind of species hence appears to be more influenced by regional than local factors, and may not be an appropriate group when one seeks to study the influence of local factors on carabids. Omnivorous species were positively influenced by soil pH: ground flora diversity is generally higher on soil with high pH (Chytrỳ et al. 2010), thus the food supply for omnivorous species is probably higher.

The null model was the most explicative for woodland eurytopic species. This finding indicates that the diversity of woodland generalist species was neither explained by local nor microenvironmental factor. On the contrary, our results showed than stenotopic forest species were sensitive to local variable. A possible interpretation would be that forest generalist species have no strict requirements within adult stands, contrary to stenotopic species. We can thus expect than stenotopic species would be more sensitive than eurytopic species to local perturbations.

Conclusions

Even though carabids are not directly affected by forest management, carabid species, thanks to their interspecific variability, present different sensitivity to stand maturity, presence of regeneration or top soil characteristics. Within a silvicultural cycle, forest management practices impact indirectly these structural characteristics, creating opportunities to establish for the different ecological groups. The conservation of adult stand could hence be necessary to preserve forest specialist species. At larger scales, we can extrapolate from our results that the creation of a structural heterogeneity resulting from forest management benefits total species richness of ground beetles. Because management practice changes the configuration of the landscape by creating open areas, it would be also interesting to consider landscape variables in future researches to explain carabid diversity.

Acknowledgments

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Tables and figures

Fig. 1 Location of the six french study sites

Table 1 Study sites characteristics and number of plot in each site; ND= undetermined

Sites	Auberive	Chizé	Citeaux	Combe Lavaux	Ventron	Ballons comtois
Coordinates	47°47'N,5°3'E	46°07'N, -O,25E	47°6'N,5,05E	47°13'N4°56'E	47°56'N,6°56'E	47°58N,6°56'E
Mean elevation (m)	440	73	200	413	920	1030
Substrate type	calcareous	calcareous	acidic	calcareous	acidic	acidic
Time since abandonment (years)	40	10	ND	30	20	>20
Forest surface area of unmanaged reserve (ha)	280	2579	29	300	300	270
Dominant stands	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
Number of plot	24	24	12	8	8	16
In unmanaged area	12	12	6	4	4	8
In managed area	12	12	6	4	4	8
Sampling period	April-June	May-July	May-July	May-July	June-August	Mid June-mid September
Year	2009	2010	2010	2010	2009	2010

Table 2 Comparaison of the explanatory variable between managed and unmanaged stands. MAN=managed plots; UNM= unmanaged plot. Chi-square tests were used for binary variable and Wilcoxon-tests for quantitative variables; n.s: non-significant result

		MAN	**UNM**	**p-value**
binary variable				
Dead wood	proportion (%)	49	51	n.s
Herbal layer	proportion (%)	51	49	n.s
Living wood	proportion (%)	53	47	n.s
quantitative variable				
Humus	mean	2.6	2.7	n.s
	standard deviation	(1.5)	(1.7)	
Sapling (number of stems/trap)	mean	2.6	2.6	n.s
	standard deviation	(5.0)	(6.7)	
Seedling (cover/trap)	mean	4.7	6.5	n.s
	standard deviation	(6.2)	(12.6)	
Stand basal area (m2/ha)	mean	21.7	23.4	n.s
	standard deviation	(7.4)	(12.3)	
pH	mean	6.0	6.1	n.s
	standard deviation	(0.9)	(0.9)	
Elevation (m)	mean	457.9	469.3	n.s
	standard deviation	(353.1)	(350.6)	

Table 3 Model selection (GLMM with quasi poisson correction) by QAICc and Akaike weights for total species richness and species richness per group (canopy-openess affinities, dispersal ability, tropic groups, moisture preferences). The model with the highest Akaike weight was systematically chosen. The QAICc and weight of the selected models are in bold characters. We ran additive models only for explanatory variable with more than 100 occurrences

			Stot	Habitat generalist	Openland	Woodland eurytopic	Woodland stenotopic	Brachypterous	Non brachypterous	Omnivorous	Carnivorous	Hygrophilous	Moisture Indifferent	Xerophilous
		Nb of occurences	265	67	76	262	249	265	84	189	263	79	265	70
[0]	null	QAICc	241.9	204.7	203.0	**181.9**	259.7	231.7	300.6	257.5	242.5	198.1	224.9	237.5
		Weights (%)	2.3	1.9	0.6	**15.1**	0.2	1.1	3.1	0.0	1.4	6.7	2.5	0.7
[1]	Elevation	QAICc	243.8	202.1	196.6	183.0	261.0	233.8	301.4	250.8	244.1	199.8	225.4	**228.2**
		Weights (%)	0.9	7.2	13.8	8.9	0.1	0.0	2.1	0.0	0.6	2.9	2.0	**72.4**
[2]	pH	QAICc	244.0	205.8	202.3	183.2	261.0	233.3	299.1	**232.3**	242.7	198.1	225.3	233.9
		Weights (%)	0.8	1.2	0.8	7.8	0.1	0.5	6.5	**100.0**	1.3	6.7	2.1	4.2
[3]	humus	QAICc	238.1	206.4	197.2	182.8	254.1	226.6	**295.3**	255.5	237.7	195.9	223.8	236.2
		Weights (%)	15.1	0.8	10.2	9.7	3.8	15.1	**43.1**	0.0	15.9	20.4	4.5	1.0
[4]	Herbal layer	QAICc	243.1	199.5	199.7	184.0	261.8	233.8	295.8	259.4	244.0	197.8	227.0	233.7
		Weights (%)	1.3	27.2	2.9	5.3	0.1	0.4	34.4	0.0	0.7	7.7	0.9	4.6
[5]	Seedling	QAICc	243.4	**198.0**	205.0	183.3	259.7	231.7	301.2	258.7	244.4	200.2	224.4	232.6
		Weights (%)	1.1	**56.6**	0.2	7.7	0.2	1.1	2.3	0.0	0.6	2.4	3.3	8.2
[6]	Sapling	QAICc	244.0	205.8	**193.6**	183.9	255.3	233.8	301.3	259.0	244.5	**195.1**	224.5	235.6
		Weights (%)	0.8	1.1	**61.0**	5.5	2.1	0.4	2.1	0.0	0.5	**30.0**	3.2	1.8
[7]	Living wood	QAICc	243.0	206.8	203.6	183.3	261.5	231.4	301.2	259.1	243.1	197.5	225.7	239.2
		Weights (%)	1.4	0.7	0.4	7.3	0.1	1.4	2.3	0.0	1.1	9.0	1.7	0.3
[8]	Dead wood	QAICc	243.5	205.4	201.0	183.3	260.9	233.7	301.7	259.5	244.3	199.2	225.9	239.0
		Weights (%)	1.0	1.4	1.5	7.7	0.1	0.4	1.8	0.0	0.6	3.9	1.6	0.3
[9]	Management	QAICc	243.0	205.8	197.6	183.5	261.0	232.8	302.4	257.5	244.5	197.9	227.0	233.2
		Weights (%)	1.3	1.2	8.1	6.8	0.1	0.7	1.2	0.0	0.5	7.3	0.9	5.8
[10]	Stand basal area	QAICc	240.8	206.7	203.4	183.8	254.1	229.6	302.6	259.6	240.4	199.7	221.4	238.9
		Weights (%)	4.1	0.7	0.4	5.9	3.8	3.3	1.1	0.0	4.1	3.0	15.0	0.3

			Stot	Habitat generalist	Openland	Woodland eurytopic	Woodland stenotopic	Brachypterous	Non brachypterous	Omnivorous	Carnivorous	Hygrophilous	Moisture Indifferent	Xerophilous
[11]		QAICc	249.2	-	-	190.1	260.8	237.1	-	265.5	250.3	-	227.8	-
		Weights (%)	0.1	-	-	0.3	0.1	0.0	-	0.0	0.0	-	0.6	-
[12]		QAICc	242.3	-	-	185.3	256.0	231.2	-	259.6	242.5	-	223.4	-
		Weights (%)	1.9	-	-	2.7	1.5	1.5	-	0.0	1.4	-	5.5	-
[13]		QAICc	250.2	-	-	191.7	262.2	238.3	-	265.7	252.3	-	230.0	-
		Weights (%)	0.0	-	-	0.1	0.1	0.0	-	0.0	0.0	-	0.2	-
[14]		QAICc	238.9	-	-	184.4	255.1	227.2	-	255.9	239.5	-	225.9	-
		Weights (%)	10.4	-	-	4.4	2.4	10.8	-	0.0	6.5	-	1.6	-
[15]		QAICc	248.2	-	-	192.1	258.6	236.0	-	267.6	248.8	-	226.7	-
		Weights (%)	0.1	-	-	0.1	0.4	0.1	-	0.0	0.1	-	1.0	-
[16]		QAICc	**235.5**	-	-	184.3	**248.1**	**223.8**	-	257.2	**234.9**	-	**218.9**	-
		Weights (%)	**56.4**	-	-	4.5	**78.8**	**61.8**	-	0.0	**63.9**	-	**51.2**	-
[17]		QAICc	245.3	-	-	190.9	255.1	232.2	-	263.4	245.6	-	226.5	-
		Weights (%)	0.4	-	-	0.2	2.4	0.7	-	0.0	0.3	-	1.1	-
[18]	Complete additive	QAICc	244.4	-	-	194.1	254.4	231.9	-	265.5	245.6	-	226.6	-
		Weights (%)	0.7	-	-	0.0	3.3	1.0	-	0.0	0.3	-	1.1	-

Table 4 Parameter estimations of the best model for each response variable derived from a generalised mixed effect model

Species traits		Best model				
		[16]	Stand basal area		Humus	
Total species richness	Estimate (SE)		0.006885	(0.002637)	-0.044784	(0.015697)
Woodland stenotopic	Estimate (SE)		0.01426	(0.00426)	-0.03938	(0.02398)
Brachypterous	Estimate (SE)		0.007146	(0.002622)	-0.037359	(0.014772)
Carnivorous	Estimate (SE)		0.007516	(0.002787)	-0.045558	(0.017433)
Moisture indifferent	Estimate (SE)		0.008474	(0.002613)	-0.028602	(0.013905)
		[6]	Sapling			
Openland	Estimate (SE)		0.037618	(0.007968)		
Hygrophilous	Estimate (SE)		0.03000	(0.01018)		
		[5]	Seedling			
Habitat generalist	Estimate (SE)		-0.05348	(0.02156)		
		[2]	pH			
Omnivorous	Estimate (SE)		0.67398	(0.05857)		
		[3]	Humus			
Not brachypterous	Estimate (SE)		-0.1418	(0.0882)		
		[1]	Elevation			
Xerophilous	Estimate (SE)		-0.0031881	(0.0007094)		

Appendices

Appendix 1 Species, abundance and characteristics of ground beetles collected in the six french forest sites; ND=undetermined

Species identities	Canopy-openess affinities	Dispersal ability	Moisture affinities	Tropic groups	abundance
Abax ovalis(Duftschmid)	woodland stenotopic	brachypterous	indifferent	carnivorous	287
Abax parallelepipedus(Piller & Mitterpacher)	woodland eurytopic	brachypterous	indifferent	carnivorous	4113
Abax parallelus(Duftschmid)	woodland stenotopic	brachypterous	indifferent	carnivorous	317
Amara ovata(Fabricius)	openland	non.brachypterous	xerophilous	mostly phytophagous	2
Badister meridionalis(Puel)	generalist	non.brachypterous	hygrophilous	carnivorous	1
Calosoma inquisitor(Linnaeus)	woodland stenotopic	non.brachypterous	indifferent	carnivorous	1
Carabus auratus(Linnaeus)	generalist	brachypterous	xerophilous	carnivorous	303
Carabus auronitens(Fabricius)	woodland stenotopic	brachypterous	indifferent	carnivorous	252
Carabus convexus(Saulcy)	openland	brachypterous	xerophilous	carnivorous	3
Carabus coriaceus(Dejean)	woodland stenotopic	brachypterous	indifferent	carnivorous	19
Carabus granulatus(Schaum)	generalist	non.brachypterous	hygrophilous	carnivorous	4
Carabus monilis(Bellier)	openland	brachypterous	hygrophilous	carnivorous	557
Carabus nemoralis(O.F. Müller)	woodland eurytopic	brachypterous	indifferent	omnivorous	511
Carabus problematicus(Vacher de Lapouge)	woodland eurytopic	brachypterous	indifferent	carnivorous	26
Carabus violaceus(Fischer von Waldheim)	woodland stenotopic	brachypterous	indifferent	carnivorous	165
Cicindela campestris(Mandl)	generalist	non.brachypterous	xerophilous	carnivorous	3
Cychrus attenuatus(Fabricius)	woodland stenotopic	brachypterous	indifferent	carnivorous	147
Cychrus caraboides(Schrank)	woodland stenotopic	brachypterous	indifferent	carnivorous	15
Harpalus atratus(Latreille)	openland	non.brachypterous	xerophilous	mostly phytophagous	11
Harpalus latus(Linnaeus)	generalist	non.brachypterous	xerophilous	mostly phytophagous	5
Leistus ferrugineus(Linnaeus)	generalist	non.brachypterous	indifferent	carnivorous	1
Leistus rufomarginatus(Duftschmid)	woodland eurytopic	non.brachypterous	indifferent	carnivorous	9
Limodromus assimilis(Paykull)	woodland stenotopic	non.brachypterous	hygrophilous	carnivorous	26
Molops piceus(Frölich)	woodland stenotopic	brachypterous	indifferent	carnivorous	34
Nebria brevicollis(Baudi di Selve)	generalist	non.brachypterous	xerophilous	carnivorous	4
Nebria salina(Fairmaire & Laboulbène)	openland	non.brachypterous	xerophilous	carnivorous	2
Notiophilus biguttatus(Fabricius)	woodland eurytopic	non.brachypterous	indifferent	carnivorous	2
Notiophilus palustris(Duftschmid)	generalist	non.brachypterous	hygrophilous	carnivorous	1
Notiophilus rufipes(Dejean)	woodland eurytopic	non.brachypterous	hygrophilous	carnivorous	4
Notiophilus substriatus(Duftschmid)	openland	non.brachypterous	xerophilous	carnivorous	1
Patrobus atrorufus(Stroem)	woodland stenotopic	brachypterous	hygrophilous	carnivorous	8
Pterostichus aethiops(Panzer)	woodland stenotopic	brachypterous	hygrophilous	carnivorous	1
Pterostichus burmeisteri(Schaum)	woodland eurytopic	brachypterous	indifferent	carnivorous	181
Pterostichus cristatus(L. Dufour)	woodland stenotopic	brachypterous	indifferent	carnivorous	266
Pterostichus madidus(Fabricius)	woodland eurytopic	brachypterous	indifferent	omnivorous	1259
Pterostichus melanarius(Illiger)	generalist	non.brachypterous	xerophilous	carnivorous	90
Pterostichus niger(Heer)	woodland eurytopic	non.brachypterous	indifferent	carnivorous	97
Pterostichus nigrita(Paykull)	generalist	non.brachypterous	hygrophilous	carnivorous	2
Pterostichus oblongopunctatus(Fabricius)	woodland eurytopic	non.brachypterous	indifferent	carnivorous	32
Pterostichus ovoideus(Sturm)	openland	brachypterous	xerophilous	omnivorous	3
Pterostichus pumilio(Dejean)	woodland eurytopic	brachypterous	indifferent	carnivorous	32
Syntomus obscuroguttatus(Duftschmid)	woodland stenotopic	non.brachypterous	indifferent	carnivorous	1
Trechus obtusus(Chaudoir)	generalist	non.brachypterous	xerophilous	carnivorous	1
Trichotichnus nitens(Linnaeus)	woodland stenotopic	non.brachypterous	indifferent	NA	3
TOTAL					8802

Appendix 2 Number of individuals and number of species for each species trait

Ecological group	Species traits	Abundance	Species richness
Canopy-openess affinities	generalist	415	11
	openland	579	7
	woodland eurytopic	6266	11
	woodland stenotopic	1542	15
Dispersal ability	brachypterous	8499	21
	non.brachypterous	303	23
Moisture affinities	xerophilous	428	12
	indifferent	7770	23
	hygrophilous	604	9
Tropic groups	mostly phytophagous	18	3
	omnivorous	1773	3
	carnivorous	7008	37

Exploitation forestière
et gradients d'habitats :
réponse des communautés de Coléoptères carabiques

Encadré par Emmanuelle Dauffy Richard et Yoan Paillet
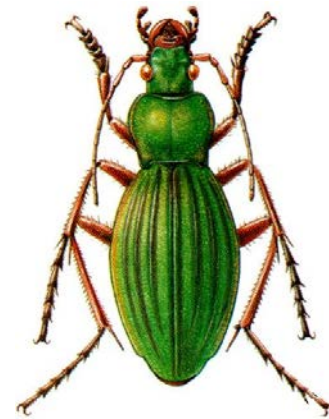
Introduction

L'exploitation forestière source de perturbation

prélèvement d'arbres	export de biomasse	circulation d'engins

ouverture de la canopée
diminution du bois mort,
cycle biogéochimique
ornières, tassements....

**Sites de reproduction
disponibilité alimentaire
microhabitats**
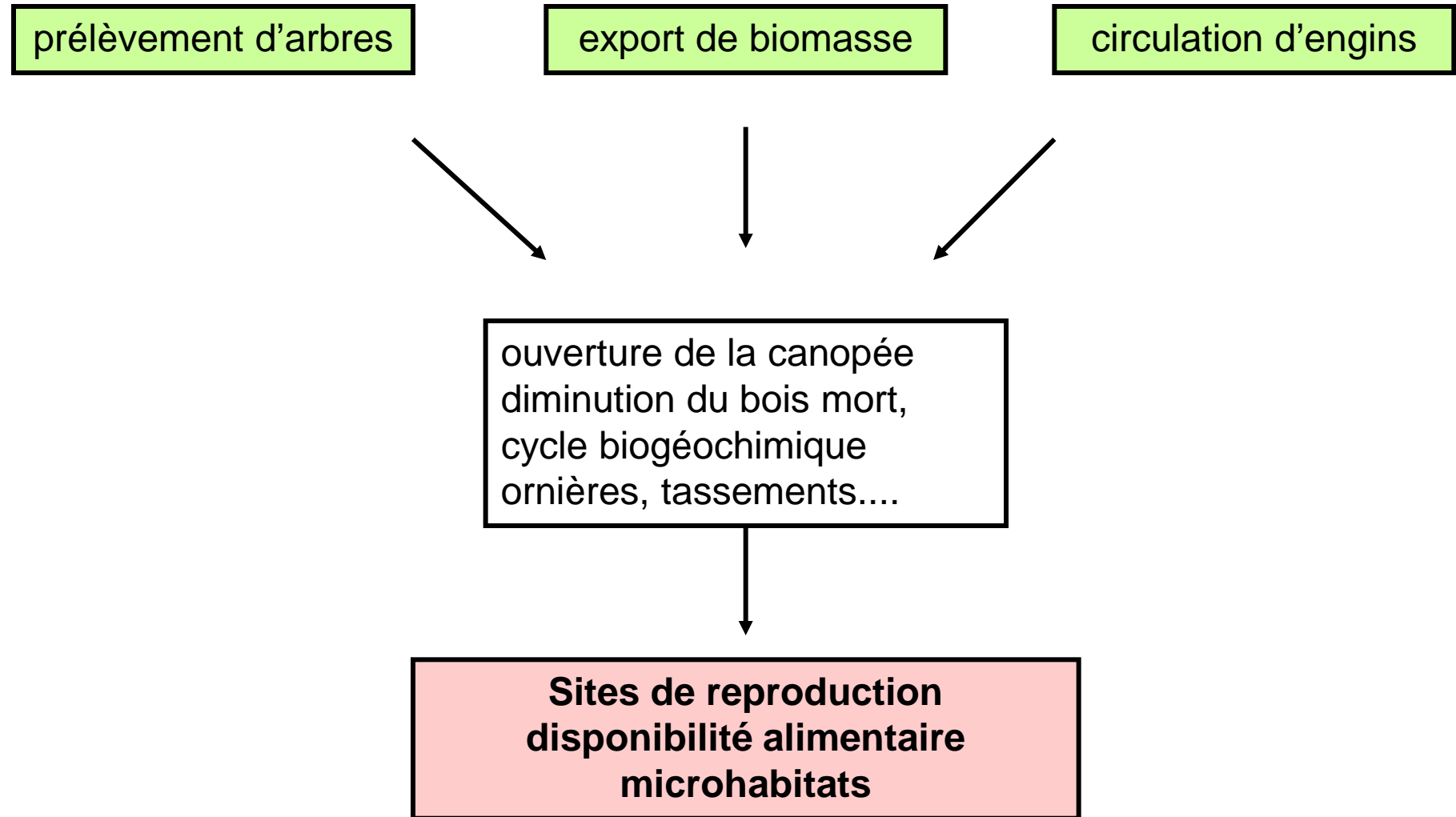
Introduction
Les carabes (Coleoptéra : carabidae)

Carabus punctatoauratus ; C. clathratus ; C.Hispanus ; C. auronitens

~1000 espèces en France

Rythmes saisonniers	**Régimes alimentaires**	**Habitats**	**Dispersion**
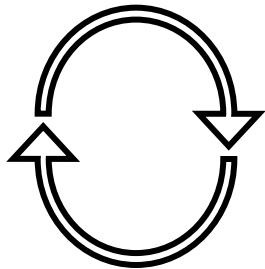
dormance

Prédateurs

Phytophages

Omnivores

ouverture/humidité

Vol

Marche

reproduction
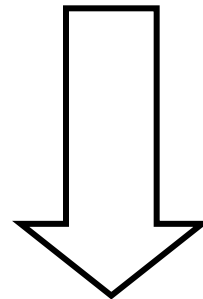
≠ Sensibilités aux changements environnementaux

Problématique et hypothèses

Problématique

> Les Coléoptères carabiques sont-ils sensibles à l'exploitation forestière?
>
> Quelles sont les relations entre les caractéristiques de l'habitat et les traits des espèces?

Hypothèses

La diversité des carabes est affectée par l'exploitation forestière. *(Paillet et al. 2010)*

La réponse des carabes aux changements de l'habitat varie selon les traits écologiques et morphologiques des espèces. *(Barbaro et al. 2009)*

Méthodes

Localisation des massifs sur le territoire Français

Méthodes

Le plan d'échantillonnage
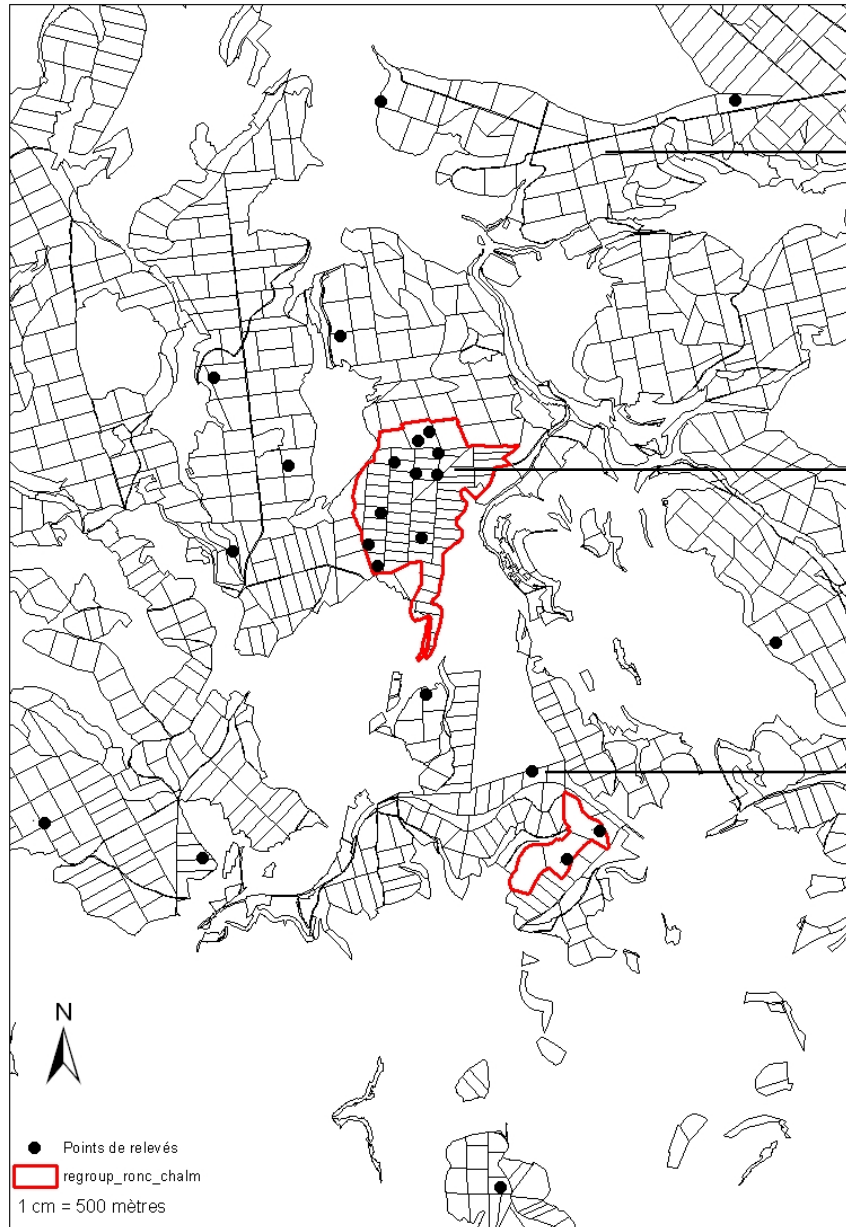
Zone exploitée

Zone non exploitée

0 gd

N

P1

10 m

P2

267 gd

P3

133 gd
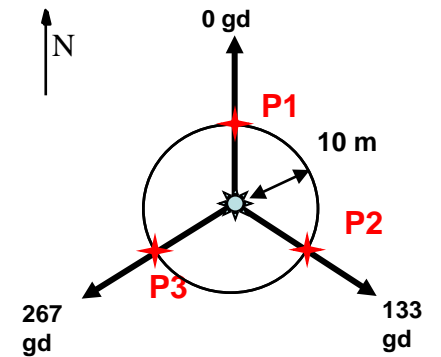
- 3 mois au printemps
- 1 relevé/mois

● Points de relevés

▭ regroup_ronc_chalm

1 cm = 500 mètres

Méthodes

Caractérisation environnementale des placettes

| Environnement du piège (1.5 – 2m) | Environnement de la placette (20m) |
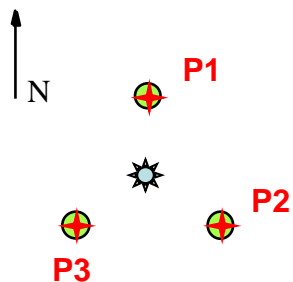
Présence/absence :

bryophytes

herbe

bois vivant
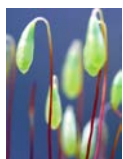
bois mort
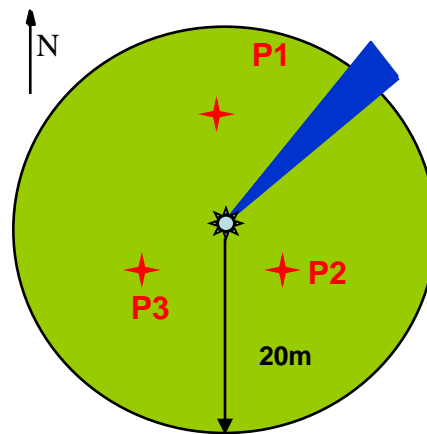
➡ **surface terrière** des arbre diamètre >20cm

➡ **humus**

Densité :

semis

régénération
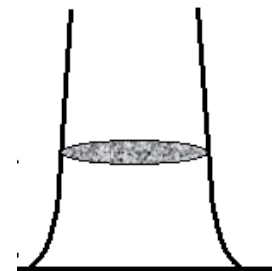
1   9
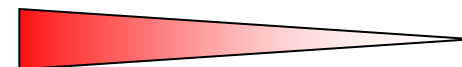
Activité biologique

➡ **pH**

➡ modalité **gérée/ non gérée**

Méthodes

L'analyse de données

variables réponses		variables explicatives

Richesse totale

RS. spécialistes forestières

RS. généralistes forestières

RS. milieu ouvert

RS. carnivores

RS. omnivores

RS. ailées

RS. aptères

$$\sim \quad \sum \alpha X + \beta + \gamma N + M|P$$

Univarié
Additif
Maximum
Nul

I(log(Nper_plot.Ptrap))

aleatoire

Résultats

Les caractéristiques de l'habitat

● **Richesse spécifique totale**
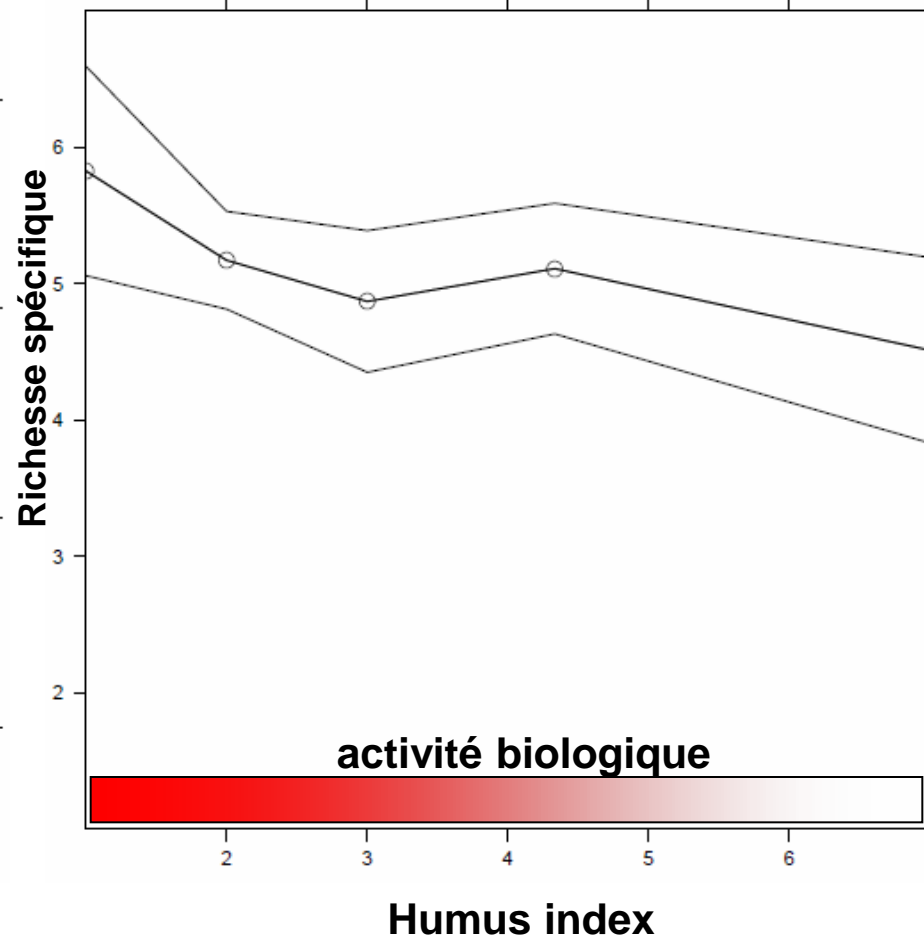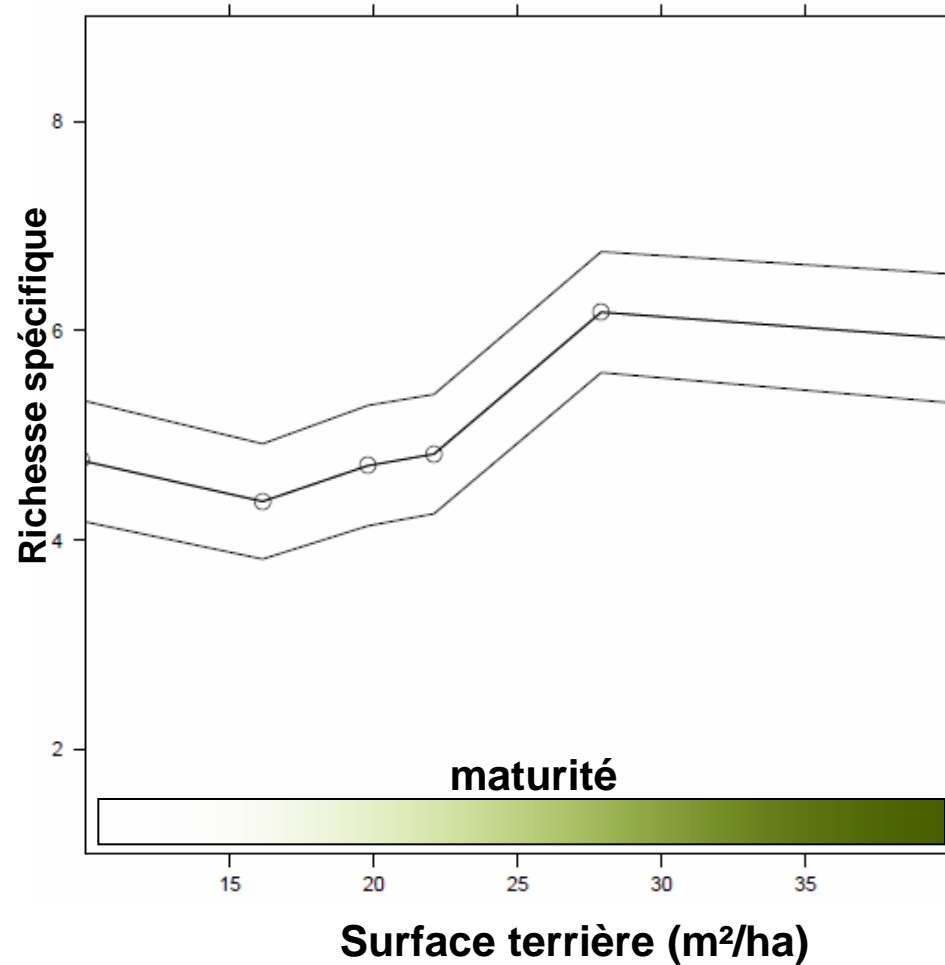
Le nombre d'espèce de carabes augmente avec: la maturité du peuplement
l'activité biologique des humus

Résultats

Les caractéristiques de l'habitat

● **Préférendum d'habitat**

surface terrière   **humus**   **Nul**   **régénération**

+ | **-** | **+**
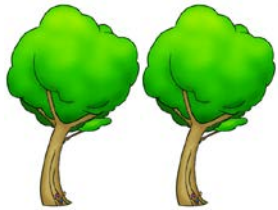
| spécialistes forestières | forestières généralistes | espèces de milieu ouvert |
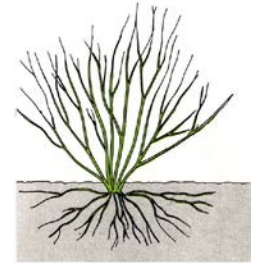
Spécialistes forestières: diversité plus importante en peuplement mature et avec des humus à activité biologique importante

Espèces de milieu ouvert: la diversité est favorisée par les trouées forestières

Résultats

Les caractéristiques de l'habitat

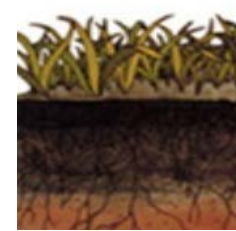● **Capacités de dispersion**
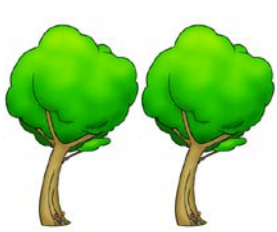
surface terrière **humus** **humus**

+ **-** **-**
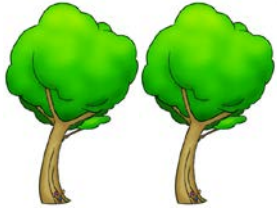
espèces aptères **espèces ailées**

Faible capacité dispersion: diversité plus importante en peuplement mature et avec des humus à activité biologique importante

Forte capacité dispersion: la diversité ne dépend pas de la maturité du peuplement

Résultats

Les caractéristiques de l'habitat

● **Groupes trophiques**

pH station

surface terrière

humus

+

-

+

| carnivores |

| omnivores |

Carnivores: diversité plus importante en peuplement mature et avec des sols à activité biologique importante

Omnivores: la diversité dépend de facteurs abiotiques

Discussion

Pas de pouvoir explicatif de l'exploitation forestière

Conditions plus contrôlées que dans les études précédentes

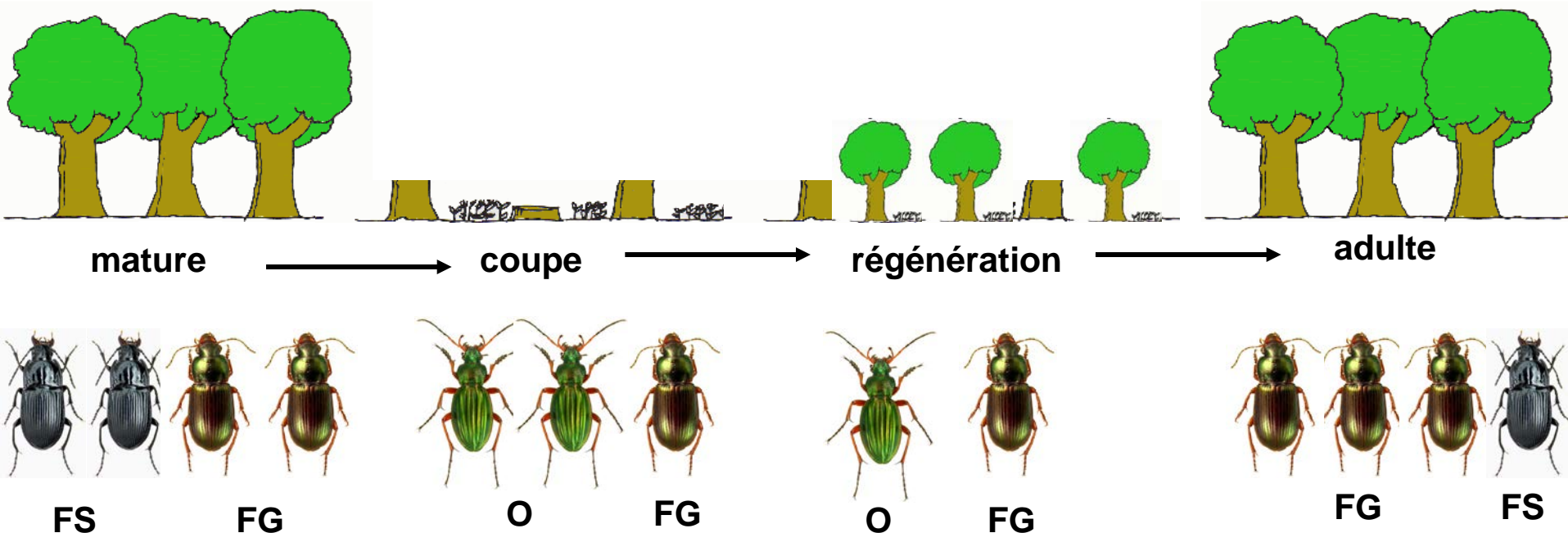$S_{\text{forêt feuillus}} > S_{\text{plantation conifères}}$

$S_{\text{régénération}} > S_{\text{forêt mature}}$

(Finch et al. 2005)

(Pool et al. 2003)

Réponse rapide des carabes aux changements du milieu

(Niemela et al. 1993)

mature → coupe → régénération → adulte

FS   FG   O   FG   O   FG   FG   FS

Discussion

Propriétés importantes de l'habitat pour le maintien de la diversité de carabes

Maturité du peuplement ⟶ **Stot; spécialistes forestières; aptères; carnivores**

Fermeture de la canopée *(Jukes et al. 2001)*

Environnement stable *(Kotze and O'Hara 2003)*

Trouées forestières ⟶ **Sp. milieu ouvert**

Turnover d'espèces *(Niemela et al. 1993)*

Humus riche ⟶ **Stot; spécialistes forestières; ailées; aptères; carnivores**

Rôle de la litière : alimentation/refuge *(Koivula et al. 1999)*
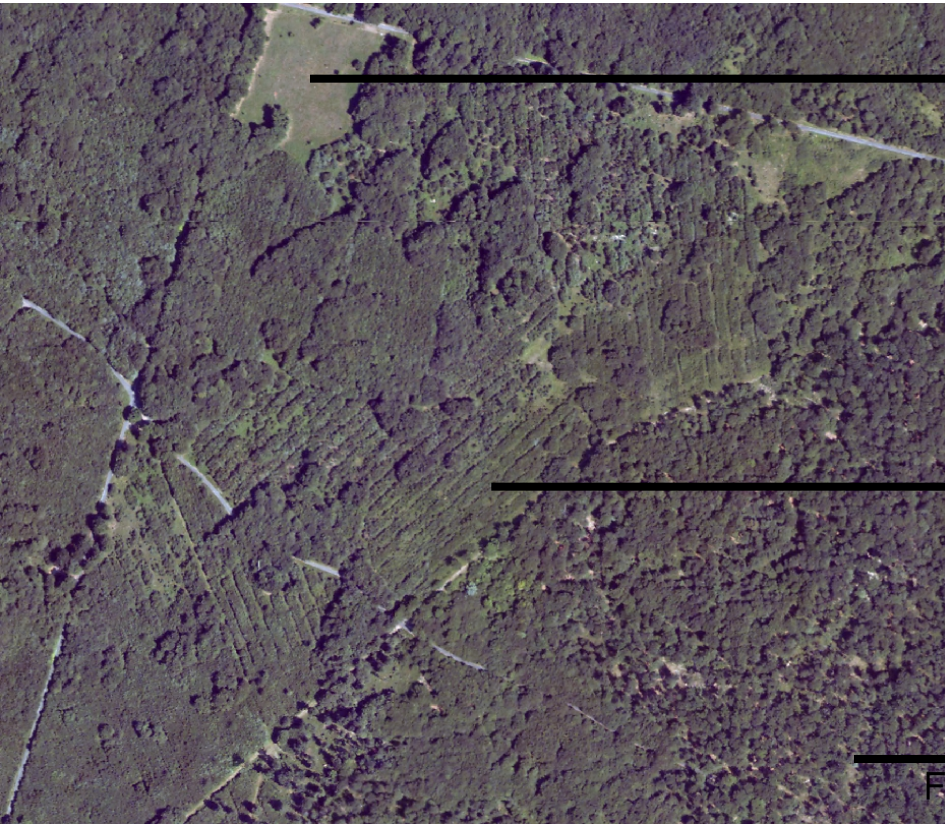
Facteurs abiotiques ⟶ **Omnivores**

Couvert floristique influencé par le pH *(Chytry et al. 2010)*

Importance de la structure de l'habitat au niveau du peuplement et du microenvironnement

Discussion

A l'échelle du paysage

Zone ouverte

Zone régénération

Peuplement adultes

Hypothèse : assemblages de carabe influencé par l'hétérogénéité du paysage

Merci pour votre attention