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Short-term response of ground beetles (Coleoptera: Carabidae) to fire and logging in a spruce-dominated boreal landscape

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Abstract

For thousands of years, fire has been the main stand-replacing disturbance in the boreal forest but is now being supplemented by logging over most of the biome's extant. Community response to such disturbances of different nature and severity has been extensively compared in plant, but rarely in animal communities. Effects of fire and logging on some groups, such as ground beetles, have been assessed but separately, in different regions and different time frames. In a single 250-km² spruce-dominated landscape in the province of Quebec, Canada, we sampled ground beetle assemblages from recently logged ($n = 12$), recently burned ($n = 12$) and control stands ($n = 18$) using pitfall traps. Our objective was to compare assemblages from recently disturbed areas of the same age and nested in the same matrix. Assemblages were not highly specific to single habitats, but diverged significantly between treatments in abundance and species dominance. Capture rates were highest in logged stands, and lowest in burned stands. Forest generalists, including *Calathus ingratus* Dejean and *Pterostichus brevicornis* (Kirby), dominated assemblages in logged stands. We suggest that the contrasting activity levels observed following these two types of disturbance and the dominance of forest generalist in logged stands may partly reflect initial mortality patterns caused by these disturbances, as fires as severe as the one sampled in this study generally result in a much higher mortality rate in soil invertebrates than logging.

1. Introduction

The concept of ecological disturbance was defined by Sousa (1984) as a "discrete, punctuated killing, displacement or damaging of individuals (...) that directly or indirectly creates an opportunity for new

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individuals (…) to become established". Either by killing individuals and/or by changing the environment to some degree, disturbance usually results in abrupt changes in community structure and can profoundly alter species succession. The subsequent evolution of the affected communities of either sessile or mobile organisms could depend on several characteristics of the disturbance, especially its severity and resulting mortality rate of organisms, the heterogeneity and structure of the new environment and its degree of connectivity to potential sources of colonists (Sousa, 1984; Peltzer et al., 2000; Spies and Turner, 2001).

For thousands of years, fire has been the main stand-replacing disturbance in the boreal forest (Zackrisson, 1977; Johnson, 1992; Payette, 1992; Bergeron et al., 2001), but is now being supplemented by logging over most of the biome's extant (Bengtsson et al., 2000; Bergeron et al., 2002). These two disturbances clearly differ both in their severity and in their respective resulting environment. While logging is expected to have at most moderate effects in terms of immediate mortality on non-target plants and less-mobile animals, forest fires have the potential to produce a whole gradient of effects depending on the nature and severity of the fire event; in the case of severe fires, very few survivors are left among ground-dwelling arthropods (Paquin and Coderre, 1997; Wikars and Schimmel, 2001). Also, the environments created by these two disturbances differ significantly on their soil structure and their associated vegetation. The organic soil layer can be greatly reduced in burns, compared to a thicker but locally more compact layer in clearcuts (Rees and Juday, 2002). Post-disturbance vegetation is mostly dominated in recent burns by fire-resistant shrubs (mostly Ericaceae), compared to a more varied set of residual mature forest species in clearcuts (Nguyen-Xuan et al., 2000). Because of these remnant small patches of forest floor, which in several cases persist, harvesting returns the site to a later successional stage than fire (Rees and Juday, 2002).

Short-term response of ground-dwelling arthropods to disturbance have been extensively studied (Seastedt and Crossley, 1981; Holliday, 1984; Martel et al., 1991; Saint-Germain and Mauffette, 2001; Wikars and Schimmel, 2001), particularly for ground beetles which have been widely used as indicators in relation to anthropogenic disturbances (Lenski, 1982; Niemelä et al., 1993; Spence et al., 1996; Beaudry

et al., 1997; Heliölä et al., 2001; Koivula and Niemelä, 2002). However, they have seldom, if ever, been documented from both clearcuts and burns from the same landscape and from disturbances of the same age and thus exposed to the same recovery conditions.

We believe that simultaneous sampling is needed to better understand disparities between the initial responses of ground beetle communities using these two disturbed environments. In this study, we sampled carabid assemblages from a 5097-ha forest fire, several logged stands and control mature stands. All disturbances were 2-year-old, and all stands were from a single, spruce-dominated landscape. Our main objectives were to compare ground beetle assemblages from clearcuts and burns 2 years after disturbance and to use assemblage data to discuss processes driving community response in ground-dwelling arthropods following fire and harvesting.

2. Materials and methods

2.1. Study area

Sampling was conducted during the summer of 2001 in a 250-km^2 landscape located about 150 km northeast of Quebec City, Que., Canada (47°41'N; 70°41'W). This landscape covered part of a 5097 ha 1999 forest fire, mainly located in the Grands–Jardins provincial park and an adjacent managed area located in the Laurentian wildlife reserve. This fire-prone landscape contains the southernmost lichen woodland of eastern Canada, a legacy of its peculiar disturbance history (Payette et al., 2000). Local vegetation is mainly composed of lichen woodlands and spruce-moss forests, dominated by black spruce *Picea mariana* (Miller), with the occasional presence of balsam fir *Abies balsamea* (L.) and tamarack *Larix laricina* (DuRoi). Herbaceous and shrub layers are mainly dominated by mosses, grasses and sedges, *Cladina* lichens and Ericaceae like *Vaccinium* spp., *Ledum groendlandicum* Oeder and *Kalmia angustifolia* L.

2.2. Sampling

In mid-May 2001, sampling plots were selected as follows: 12 burned plots in the Grands–Jardins

provincial park, 2-year-old (12) logged plots in the adjacent Laurentian wildlife reserve and 18 mature forest control plots, equally scattered in both areas. The Grands–Jardins 1999 forest fire was especially severe and uniform. Burned plots sampled had no surviving trees or unscorched ground areas. The logged stands from the Laurentian wildlife reserve were harvested by clearcut. There was a minimum distance of 500 m between plots of the same group, and disturbed plots were situated at least 30 m from the forest edge. Sampling plots consisted of a 400-m^2 area through which a transect of three pitfall traps was established, with 10 m between each trap. Pitfall traps used consisted of covered 10-cm diameter plastic cups and were unbaited. Because we had to restrict our sampling period, traps were activated for 6 weeks between June 6 and July 17 to cover the main activity peak of carabids in Quebec as described by Lévesque and Lévesque (1986). Traps were serviced weekly, using 100 ml of 50% ethylene glycol as a preservative solution. All carabid beetles were identified to species using (Lindroth, 1961, 1963, 1966, 1968, 1969) and identifications were cross-checked at the Canadian National Collection of insects, arachnids and nematodes (Ottawa, Canada) and at the Ouellet–Robert entomological collection (University of Montreal, Montreal, Canada). Vouchers are deposited at the Lyman Entomological Museum (McGill University, Montreal, Canada). Measures of moss depth, litter depth, bare soil cover, lichen/moss cover, ground vegetation cover and canopy cover were taken for all sample plots.

2.3. Statistical analyses

Carabid species richness, standardized capture rates (captures/trap/week) and stand characterization variables were compared between treatments using one-way analyses of variance and Tukey's HSD post hoc tests. Data were log-transformed to meet normality and homogeneity of variance assumptions. Species richness was also compared between treatments using individual-based rarefaction curves. This technique is based on random re-sampling of the pool of captured individuals and is used to estimate expected richness at lower sample sizes (Gotelli and Colwell, 2001). Such curves are especially useful to correct for sampling effort, in cases where frequent

trap disturbance may have occurred (Buddle et al., 2005). Non-metric multidimensional scaling (NMS) was used to illustrate variations in species composition and assemblage structure among sampling sites. Confidence ellipses (1S.D.) were calculated for control, burn and cut plots and displayed on the scatterplot showing the two dimensions explaining the most variability. Mean sample scores of the three treatments along axes 1 and 2 from the NMS were compared with an analysis of variance to discriminate more objectively between assemblages. Linear regressions were used to relate measured environmental variables with the environmental gradients produced by the NMS. Analyses of variance and regressions were performed using SPSS 10.0.5 for Windows (SPSS Inc., Chicago, IL). Rarefaction curves were performed using EcoSim (Acquired Intelligence Inc. and Kesey–Bear, Burlington, VT). NMS was performed using PCOrd 4.17 (MJM Software Design Inc., Gleneden Beach, OR).

3. Results

A total of 36 species and 943 individuals of ground beetles were collected. Habitat generalist *Pterostichus adstrictus* and forest generalists *Calathus ingratus* and *Pterostichus brevicornis* dominated the assemblages and represented 60.3% of the total captures. These three species were caught in all three treatments.

Capture rates (individuals/trap/week) varied significantly between treatments ($F_{2,39} = 8.22$; $p = 0.001$). Capture rates were much lower in burned plots and were significantly lower than those from logged plots (average ± 1S.D.—burn, 0.40 ± 0.29; logged, 2.36 ± 1.24; control, 1.78 ± 4.91) (Fig. 1a). Logged plots had significantly higher species richness than burned and control plots ($F_{2,39} = 12.37$; $p < 0.001$) (Fig. 1b). However, rarefied species richness at 79 individuals (burned plots total) was highest in burned plots with logged plots second highest and controls lowest and rarefied species richness at 357 individuals (total of control plots) was higher in logged plots than in controls (Fig. 2).

Another prominent result was the dominance of forest generalists (i.e. *C. ingratus*, *P. adstrictus*, *Pterostichus punctatissimus*) and the absence of open-habitat specialists in the logged plots. This
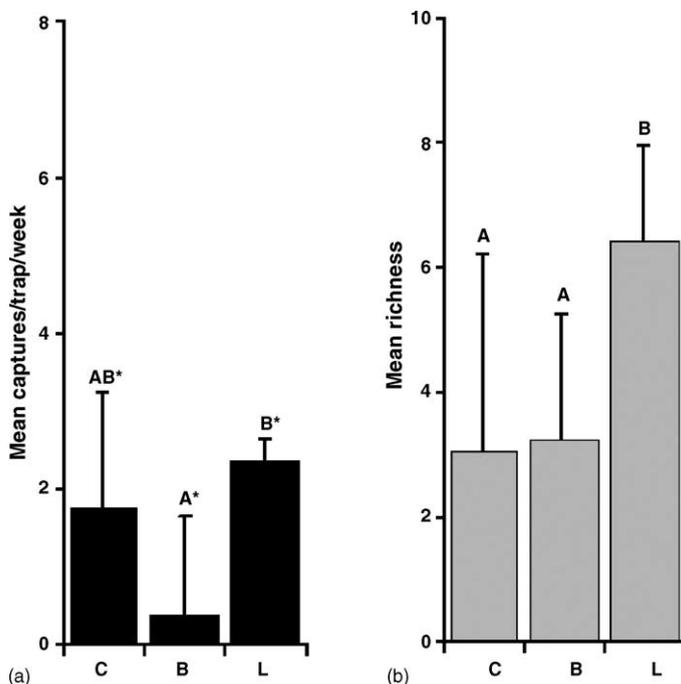
Fig. 1. Mean captures/trap/week (a) and mean richness (b) of carabids with 1S.D. for control (C), burned (B) and logged (L) plots. Letters indicate significant differences (ANOVAs and Tukey's HSD). Results with asterisks were obtained from log-transformed data.

pattern was reflected in the NMS, in which logged plot assemblages confidence ellipse was entirely contained by the controls ellipse; also, sample scores of assemblages from logged plots and controls along axes 1 or 2 were not significantly different. Burned-plot assemblages sample scores were significantly
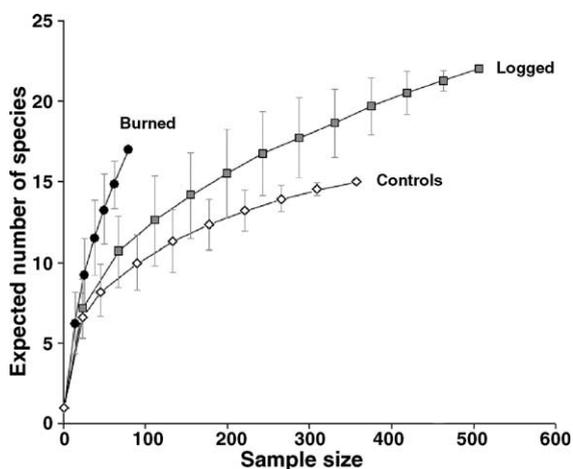

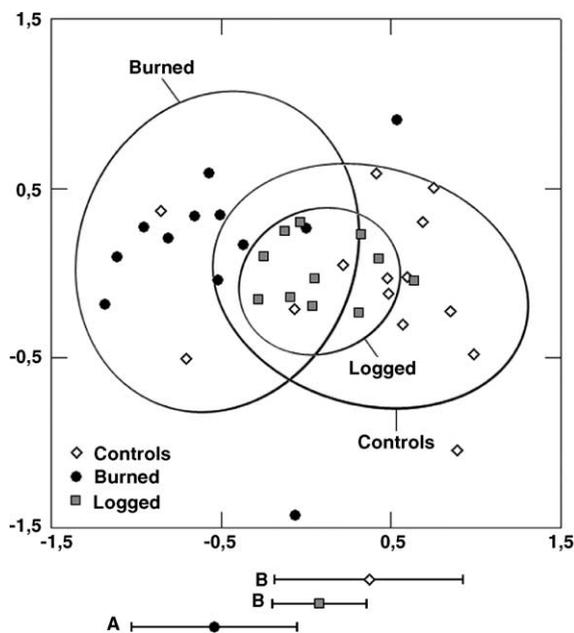Fig. 2. Individual-based rarefaction curves for carabidae caught in control, burned and logged plots.

Fig. 3. Sample scores with 1S.D. confidence ellipses for carabid assemblages from control, burned and logged plots along the two NMS axes explaining the most variability and at bottom mean sample scores for each treatments with 1S.D.

different from both logged plots and controls along axis 1 ($F_{2,35} = 11.91$; $p < 0.001$; Fig. 3). The three-dimensional solution given by the NMS explained 73.1% of the variability.

No fire specialist was abundantly captured in burned plots. However, these plots had the highest number of unique species (i.e. restricted to one plot group); these were *Cicindella longilabris*, *Cymindis unicolor*, *Notiophilus aeneus*, *Olisthopus parmatus*, *Sericoda obsoleta*, *Sericoda quadripunctata* and *Syntomus americanus*. Although *N. aeneus*, *O. parmatus*, *S. obsoleta* and

S. quadripunctata were all singletons, the latter two are well-known pyrophilous species (Richardson and Holliday, 1982; Holliday, 1984). Also, *N. aeneus* and *S. americanus* are known as xeric open-habitat species, and they might use burns on a regular basis. Six species were captured only in logged plots, of which four were singletons (Table 1).

Significant differences between treatments were detected for moss depth ($F_{2,39} = 18.08$; $p < 0.001$; highest in controls), lichen/moss cover ($F_{2,39} = 19.70$; $p < 0.001$; highest in controls, lowest in clearcuts),

Table 1

Standardized mean numbers of captures per plot ± 1S.D. and total number per species for all carabids caught in control, burned and logged plots

Species	Controls ($n = 18$)	Burned ($n = 12$)	Logged ($n = 12$)	Total
Agonum affine Kirby	0	0	0.08 ± 0.29	1
Agonum cupreum Dejean	0	0.08 ± 0.29	0	1
Agonum gratiosum (Mannerheim)	0.14 ± 0.41	0.09 ± 0.31	0.08 ± 0.29	4
Agonum metallescens (LeConte)	0	0	0.08 ± 0.29	1
Agonum retractum LeConte	0.15 ± 0.65	0	0	2
Amara erratica (Duftschmid)	0	0	0.17 ± 0.40	2
Bembidion bruxellense Wesmael	0	0	0.62 ± 2.14	7
Bembidion grapei Gyllenhal	0	0.08 ± 0.29	1.26 ± 2.01	16
Bembidion incrematum LeConte	0	0	0.08 ± 0.29	1
Bembidion occultator Notman	0	0	0.08 ± 0.29	1
Bembidion sordidum (Kirby)	0	0	0.08 ± 0.29	1
Calathus advena (LeConte)	13.78 ± 56.97	0	2.50 ± 5.65	157
Calathus ingratus Dejean	4.60 ± 12.58	0.66 ± 1.34	7.59 ± 13.00	149
Cicindela duodecimguttata Dejean	0	0	0.09 ± 0.31	1
Cicindela longilabris Say	0	0.21 ± 0.50	0	2
Cymindis cribricollis Dejean	0.06 ± 0.24	0.08 ± 0.29	0	2
Cymindis unicolor Kirby	0	0.25 ± 0.45	0	3
Harpalus nigritarsis CRSahlberg	0	0.13 ± 0.43	0.17 ± 0.39	3
Harpalus solitaris Dejean	0	0.17 ± 0.40	0	2
Harpalus somnulentus Dejean	0	0	0.08 ± 0.29	1
Notiophilus aeneus (Herbst)	0	0.08 ± 0.29	0	1
Olisthopus parmatus (Say)	0	0.09 ± 0.31	0	1
Patrobus foveocollis (Eschscholtz)	0.06 ± 0.24	0	0	1
Platynus decentis (Say)	0.06 ± 0.24	0	0.17 ± 0.58	3
Pterostichus adstrictus Eschscholtz	0.69 ± 1.36	3.37 ± 3.04	14.87 ± 7.87	224
Pterostichus brevicornis (Kirby)	6.82 ± 12.37	0.65 ± 0.98	8.59 ± 9.61	196
Pterostichus punctatissimus (Randall)	1.15 ± 1.55	0.60 ± 1.30	2.94 ± 2.78	57
Scaphinotus bilobus (Say)	0.20 ± 0.85	0	0	3
Sericoda obsoleta (Say)	0	0.09 ± 0.31	0	1
Sericoda quadripunctata (DeGeer)	0	0.09 ± 0.31	0	1
Sphaeroderus nitidicollis Chevrolat	0.12 ± 0.36	0	0	2
Stereocerus haematopus (Dejean)	2.25 ± 7.15	0	1.75 ± 3.79	44
Syntomus americanus (Dejean)	0	0.38 ± 0.90	0	4
Trechus apicalis Motschulsky	0	0	0.17 ± 0.58	2
Trechus crassicarpus Lindroth	1.86 ± 6.33	0	0.68 ± 1.02	40
Trechus rubens (Fabricius)	0.11 ± 0.47	0	0.34 ± 0.89	6
Total	357	79	507	943

ground vegetation cover ($F_{2,39} = 5.52$; $p = 0.008$; highest in burns) and canopy cover ($F_{2,39} = 81.54$; $p < 0.001$; highest in controls). Variables correlated to NMS axis 1 were moss depth ($F = 5.83$; $R^2 = 0.132$; $p = 0.021$), litter depth ($F = 4.59$; $R^2 = 0.113$; $p = 0.039$), lichen/moss cover ($F = 7.36$; $R^2 = 0.170$; $p = 0.010$) and canopy ($F = 6.14$; $R^2 = 0.146$; $p = 0.018$). None of the measured variables were correlated to axis 2, and only moss depth was correlated to axis 3 ($F = 4.43$; $R^2 = 0.110$; $p = 0.042$).

4. Discussion

Three patterns stand out from our results: the low abundance of carabids in burned plots, the absence of fire specialists from the 2-year-old burn and the dominance of forest generalists in logged plots.

Although several species of the genera *Sericoda* and *Harpalus* have been consistently associated with recent burns (Lindroth, 1966; Evans, 1971; Richardson and Holliday, 1982; Holliday, 1984; Muona and Rutanen, 1994), no such species were commonly captured in our burned plots. It has been suggested that some fire specialists (e.g. *Sericoda*) use recently burned forests for short periods of time (1–2 years) (Holliday, 1984, 1991a,b). Although this study presents only data for the second year after the fire, and hence, could have missed their peak in occurrence, another inventory taking place during the first year after fire did not record either any specimens of *Sericoda* (G. Pelletier, Canadian Forest Service, unpublished data). Also, our sampling period might not have covered the main seasonal activity peak of *Sericoda*, which is known for its early reproduction. However, this hypothesis is unlikely, since the snow cover in this region disappears around mid-May. It is also very unlikely that the low capture rates observed in burned plots result from a sampling bias between treatments related to the use of pitfall traps. Characterization data have shown that the microtopography of burned plots is not rougher than in logged plots. Also, the warmer microclimate found in burns (dark soil color) should result in higher activity levels in ground-dwelling insects (see Muona and Rutanen, 1994). Such a bias would result in capture rates higher than expected from real beetle density

alone. It is, thus, probable that the observed low capture rates illustrate lower insect densities.

Our results from logged plots are only partly consistent with what is suggested in the literature. Niemelä et al. (1993) have derived, from their results and other studies, three general responses of ground beetles to logging. First, there is an increase in open-habitat species. Second, forest generalists decrease but usually recover with forest regeneration. Third, forest specialists decrease in abundance and may fail to recolonize regenerating stands. As expected, forest specialists were rare in our logged plots. *Calathus advena* was the main forest specialist found in our landscape and represented only 5.9% of catches in logged plots, compared to 35.5% in control plots. *Trechus crassicarpus* also showed a similar trend. However, no open-habitat species was abundantly caught in our logged plots. All common species were either forest generalists (*C. ingratus*, *P. brevicornis*, *P. punctatissimus*, *Stereocerus haematopus*) or habitat generalists (*P. adstrictus*). All of these species were also frequently collected in control plots.

Results obtained by Niemelä et al. (1993) suggest that more time may be needed for open-habitat species to establish in high numbers in a recently opened habitat, as such a response was mostly noted in their study several years after the disturbance. Also, another explanation for the absence of open-habitat species could be that the studied landscape does not include other major types of open habitats besides burns and clearcuts (i.e. agricultural land), and that logging operations in the region are relatively recent (since the 1950s). The landscape, as it evolved over the last hundreds of years, may not have been able to consistently sustain open-habitat specialists, and recent land use has not yet permitted infiltration of such species.

Koivula and Niemelä (2002) have proposed several hypotheses to explain why forest generalists are in some cases common in logged stands. First, they suggested that some individuals might be wanderers from adjacent mature stands. Some species may also be present in the disturbance, but are in reality on their way to local extinction, as some carabids may live as long as 2–3 years and subsist without reproducing. Finally, some forest species might be adapted to the disturbance regime and be able to survive and proliferate in such conditions. Although some species

were caught in our study in numbers that might support the first two hypotheses, *C. ingratus*, *P. adstrictus* and *P. brevicornis* were obviously too numerous to be declining and have taken advantage of the newly created conditions.

The low capture rates in burned plots and the dominance of forest generalists in logged plots may indicate that the severity of the disturbance can have a non-negligible effect on the species composition of early post-disturbance communities. Residual populations that are left following the disturbance may have an important impact on the recovery of the community (e.g. Gandhi et al., 2001), as the few forest species that are able to tolerate the newly open environment may proliferate as more specialized species are eliminated. These residual populations are much larger in logged plots than in burns. In a comparative study, deforestation lowered soil macroarthropod abundance on average by 55%, compared to 95.5% following fire (Paquin and Coderre, 1997). Wikars and Schimmel (2001) reported a comparable mortality rate from another forest fire, while Battigelli et al. (2004) observed a mere 20% average mortality rate following harvesting. Such differences in residual population levels could partly explain why forest generalists were so abundant in logged plots and merely present in burned plots. These patterns have also been uncovered for spider communities in young burns and clearcuts in central Alberta (Buddle et al., 2000).

Colonization can also represent an important input of individuals following a disturbance. Again, fire differs from logging by producing smoke and heat that can be used as long-range attractants by adapted organisms (Evans, 1971; McCullough et al., 1998). The most distinctive elements of the fire-associated fauna are species that use these signals to converge towards the newly created habitat, as species of the genus *Sericoda* do. Such a behavior may have made possible specialization in open-habitat use in landscapes where such habitats are rare and are almost always created by fire, even if no particular habitat features exclusive to burns are sought after. These species have, however, no mechanism for converging towards recently logged areas and may end up in such areas only by wandering randomly through the landscape. Hence, logged stand communities would be mainly composed of large populations of forest generalists originating from residuals of the destroyed

ecosystem in addition to several uncommon species of various ecological affinities that stumbled upon these habitats through random dispersal. Burned stand communities, on the other hand, would be constituted of largely the same species brought about through random dispersal, in addition to more common pyrophilous species in the first 1–3 years following disturbance.

While the 1999 fire in our study area was severe, burning most of the ground vegetation, variation in the severity of wildfires is a common phenomenon in northern conifer forests given that they often extend over large areas and burn for several days (Turner and Romme, 1994; Kafka et al., 2001; Bergeron et al., 2002). The differences in ground beetle community structure that we observed between disturbance types (wildfire–timber harvesting) may thus not reflect the range of responses that these organisms may show in other wildfires. Our results suggest that disturbance may impact the subsequent recovery of carabid communities not only by producing divergent local habitat characteristics but also by producing through its inherent characteristics (i.e. severity and its impact on instant mortality) different initial post-disturbance communities. Buddle et al. (2000) have shown that such divergence in species composition can last for long periods of time. In their study, spider assemblages from post-harvest and post-fire stands converged in species composition about 30 years following disturbance. This also suggests that local disturbance history should be taken into account in biodiversity studies.

Acknowledgements

References

Battigelli, J.P., Spence, J.R., Langor, D.W., Berch, S.W., 2004. Short-term impact of forest soil compaction and organic matter removal on soil mesofauna density and oribatid mite diversity. Can. J. For. Res. 34, 1136–1149.

Beaudry, S., Duchesne, L.C., Côté, B., 1997. Short-term effects of three forestry practices on carabid assemblages in a jack pine forest. Can. J. For. Res. 27, 2065–2071.

Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. For. Ecol. Manage. 132, 39–50.

Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P., Lesieur, D., 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. Can. J. For. Res. 31, 384–391.

Bergeron, Y., Leduc, A., Harvey, B., Gauthier, S., 2002. Natural fire regime: a guide for sustainable management of the Canadian boreal forest. Sylva Fennica 36, 81–95.

Buddle, C.M., Spence, J.R., Langor, D.W., 2000. Succession of boreal forest spider assemblages following wildfire and harvesting. Ecography 23, 423–436.

Buddle, C.M., Beguin, J., Bolduc, E., Mercado, A., Sackett, T.E., Selby, R.D., Varady-Szabo, H., Zeran, R.M., 2005. The importance and use of taxon sampling curves for comparative biodiversity research with forest arthropod assemblages. Can. Entomol. 137, 120–127.

Evans, W.G., 1971. The attraction of insects to forest fires. In: Proceedings of the Tall Timbers Conference on Ecological Animal Control by Habitat Management, Tall Timbers Research Station, Tallahassee, FL, pp. 115–127.

Gandhi, K.J.K., Spence, J.R., Langor, D.W., Morgantini, L.E., 2001. Fire residuals as habitat reserves for epigaeic beetles (Coleoptera: Carabidae and Staphylinidae). Biol. Conserv. 102, 131–141.

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and composition of species richness. Ecol. Lett. 4, 379–391.

Heliölä, J., Koivula, M., Niemelä, J., 2001. Distribution of carabid beetles (Coleoptera Carabidae) across a boreal forest-clearcut ecotone. Conserv. Biol. 15, 370–377.

Holliday, N.J., 1984. Carabid beetles (Coleoptera: Carabidae) from a burned spruce forest (*Picea* spp.). Can. Entomol. 116, 919–922.

Holliday, N.J., 1991a. The carabid fauna (Coleoptera: Carabidae) during postfire regeneration of boreal forest: properties and dynamics of species assemblages. Can. J. Zool. 70, 440–452.

Holliday, N.J., 1991b. Species responses of carabid beetles (Coleoptera: Carabidae) during post-fire regeneration of boreal forest. Can. Entomol. 123, 1369–1389.

Johnson, E.A., 1992. Fire and Vegetation Dynamics: Studies from the North American Boreal Forest. Cambridge University Press, Cambridge, UK.

Kafka, V., Gauthier, S., Bergeron, Y., 2001. Fire impacts and crowning in the boreal forest: study of a large wildfire in western Quebec. Int. J. Wildland Fire 10, 119–127.

Koivula, M., Niemelä, J., 2002. Boreal carabid beetles (Coleoptera Carabidae) in managed spruce forests: a summary of Finnish case studies. Silva Fennica 36, 423–436.

Lenski, R.E., 1982. The impact of forest cutting on the diversity of ground beetles (Coleoptera: Carabidae) in the southern Appalachians. Ecol. Entomol. 7, 385–390.

Lévesque, C., Lévesque, G.-Y., 1986. Activité et succession saisonnière de coléoptères épigés d'une forêt décidue du sud du Québec. Naturaliste Can. 113, 39–45.

Lindroth, C.H., 1961. The ground-beetles (Carabidae excl Cicindelinae) of Canada and Alaska. Part 2. Opusc. Entomol. Suppl. 20, 1–200.

Lindroth, C.H., 1963. The ground-beetles (Carabidae excl Cicindelinae) of Canada and Alaska. Part 3. Opusc. Entomol. Suppl. 24, 201–408.

Lindroth, C.H., 1966. The ground-beetles (Carabidae excl Cicindelinae) of Canada and Alaska. Part 4. Opusc. Entomol. Suppl. 29, 409–648.

Lindroth, C.H., 1968. The ground-beetles (Carabidae excl Cicindelinae) of Canada and Alaska. Part 5. Opusc. Entomol. Suppl. 33, 649–944.

Lindroth, C.H., 1969. The ground-beetles (Carabidae excl Cicindelinae) of Canada and Alaska. Part 6. Opusc. Entomol. Suppl. 34, 945–1192.

Martel, J., Mauffette, Y., Tousignant, S., 1991. Secondary effects of canopy dieback: the epigeal carabid fauna in Québec Appalachian maple forests. Can. Entomol. 123, 851–859.

McCullough, D.G., Werner, R.A., Neumann, D., 1998. Fire and insects in northern and boreal forest ecosystems of North America. Annu. Rev. Entomol. 43, 107–127.

Muona, J., Rutanen, I., 1994. The short-term impact of fire on the beetle fauna in boreal coniferous forest. Ann. Zool. Fenn. 31, 109–121.

Niemelä, J., Langor, D., Spence, J.R., 1993. Effects of clearcut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. Conserv. Biol. 7, 551–561.

Nguyen-Xuan, T., Bergeron, Y., Simard, D., Fyles, J.W., Paré, D., 2000. The importance of forest floor disturbance in the early regeneration patterns of the boreal forest of western and central Quebec: a wildfire versus logging comparison. Can. J. For. Res. 30, 1353–1364.

Paquin, P., Coderre, D., 1997. Deforestation and fire impact on edaphic insect larvae and other macroarthropods. Environ. Entomol. 26, 21–30.

Payette, S., 1992. Fire as a controlling process in the North American boreal forest. In: Shugart, H.H., Leemans, R., Bonan, G.B. (Eds.), A Systems Analysis of the Boreal Forest. Cambridge University Press, Cambridge, UK.

Payette, S., Bhiry, N., Delwaide, A., Simard, M., 2000. Origin of the lichen woodland at its southern range limit in eastern Canada: the catastrophic impact of insect defoliators and fire on the spruce-moss forest. Can. J. For. Res. 30, 288–305.

Peltzer, D.A., Bast, M.L., Wilson, S.D., Gerry, A.K., 2000. Plant diversity and tree response following contrasting disturbances in boreal forest. For. Ecol. Manage. 127, 191–203.

Rees, R.C., Juday, G.P., 2002. Plant species diversity on logged versus burned sites in central Alaska. For. Ecol. Manage. 155, 291–302.

Richardson, R.J., Holliday, N.J., 1982. Occurrence of carabid beetles (Coleoptera: Carabidae) in a boreal forest damaged by fire. Can. Entomol. 113, 509–514.

Saint-Germain, M., Mauffette, Y., 2001. Reduced ground beetle activity following ice damage in maple stands of southwestern Quebec. For. Chron. 77, 651–656.

Seastedt, T.R., Crossley, D.A., 1981. Microarthropod response following cable logging and clear-cutting in the southern Appalachians. Ecology 62, 126–135.

Sousa, W.P., 1984. The role of disturbance in natural communities. Annu. Rev. Ecol. Syst. 15, 353–391.

Spence, J.R., Langor, D.W., Niemelä, J., Cárcamo, H.A., Currie, C.R., 1996. Northern forestry and carabids: the case for concern about old-growth species. Ann. Zool. Fenn. 33, 173–184.

Spies, T.A., Turner, M.G., 2001. Dynamic forest mosaics. In: Hunter, Jr., M.L. (Ed.), Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, NY.

Turner, M.G., Romme, W.H., 1994. Landscape dynamics in crown fire ecosystems. Landscape Ecol. 9, 59–77.

Wikars, L.-O., Schimmel, J., 2001. Immediate effects of fire-severity on soil invertebrates in cut and uncut pine forests. For. Ecol. Manage. 141, 189–200.

Zackrisson, O., 1977. Influence of forest fires on the north Swedish boreal forest. Oikos 29, 22–32.