J. For. Res. (2016) 27(5):1191–1202
DOI 10.1007/s11676-016-0252-z

ORIGINAL PAPER

Does variable stand structure associated with multi-cohort forests support diversity of ground beetle (Coleoptera, Carabidae) communities in the central Nearctic boreal forest?

Erica P. Barkley[1] · **Jay R. Malcolm**[1] · **Sandy M. Smith**[1] · **M. Isabel Bellocq**[2]

Received: 6 September 2014 / Accepted: 30 July 2015 / Published online: 6 May 2016

Abstract Multi-cohort management (MCM) that retains a range of stand structures (age and size class) has been proposed to emulate natural disturbance and improve management in the Nearctic boreal forest. Although MCM forests contain both single- and multi-aged stands of mixed tree sizes, little is known about how variable stand structure affects associated fauna and biodiversity. Here, we examine the relationship between ground beetle (Coleoptera, Carabidae) communities and stand characteristics across a range of forest structure (=cohort classes). Given that MCM classes are defined by the distribution of their tree–stem diameters, we ask whether parameters associated with these distributions (Weibull) could explain observed variation in carabid communities, and if so, how this compares to traditional habitat variables such as stand age, foliage complexity or volume of downed woody debris. We sampled carabids using weekly pitfall collections and compared these with structural habitat variables across a range of cohort classes (stand structure and age since disturbance) in 18 sites of upland mixed boreal forests from central Canada. Results showed that richness and diversity of carabid communities were similar among cohort classes. Weibull parameters from the diameter distribution of all stems were the strongest predictors of variation in carabid communities among sites, but vertical foliage complexity, understory thickness, and percentage of deciduous composition were also significant. The abundance of several carabid forest specialists was strongly correlated with tree canopy height, the presence of large trees, and high vertical foliage complexity. Our results demonstrate that variable forest structure, as expected under MCM, may be useful in retaining the natural range of ground beetle species across the central Nearctic boreal forest.

Keywords Biodiversity conservation · Boreal forest · Carabidae · Forest structure · Ground beetles · Multi-cohort management · Tree diameter distribution

Introduction

Periodic disturbance is a well-known driver in natural ecosystem dynamics, yet our understanding as to the impact of different disturbance regimes on the biodiversity of forested landscapes is still relatively unknown. Silvicultural techniques that emulate natural disturbance have been proposed to maintain forest biodiversity (Attiwill 1994; Bergeron and Harvey 1997) with the goal to mimic the size, frequency and intensity of the natural disturbance that species are adapted to, thereby increasing their chances of persistence on the landscape. Main natural disturbances in Nearctic boreal forests include fire, ice storms, and insect outbreaks (Bergeron et al. 2001). Currently, fire is thought to be the primary driver, having significant

---

Project Funding funding was provided by the Forestry Futures Trust, Tembec, Inc., Lake Abitibi Model Forest, Ontario Ministry of Natural Resources, National Science and Engineering Research Council of Canada, and the University of Toronto.

Corresponding Editor: Chai Ruihai

✉ Sandy M. Smith
s.smith.a@utoronto.ca

[1] Faculty of Forestry, University of Toronto, 33 Willcocks Street, Toronto, ON M5S 3B3, Canada

[2] Departamento de Ecología, Genética y Evolución, IEGEBA (CONICET-UBA), Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina

influence on tree species distributions, age-class distributions, productivity, and wildlife habitat characteristics (Bergeron et al. 2007). The early generalization that boreal forests are subject to relatively short fire cycles has been used to support clear-cutting on a relatively short (c. 100-year) rotation, resulting in even-aged, homogenous forests. However, reconstruction of fire histories in the Nearctic boreal forest suggests that fire cycles are much longer, with many stands escaping fire for 200–300 years (Bergeron et al. 2001). As a result, over half of the unmanaged Nearctic boreal forests are now composed of old-growth stands and stands with multiple cohorts of trees.

In the late 1990s, multi-cohort management (MCM) was proposed to better emulate natural disturbance in the Canadian boreal forest. Under MCM, diverse silvicultural techniques are used to achieve a range of structural variation emulating three broad successive phases of post-fire development or "cohort classes" (Bergeron and Harvey 1997; Bergeron et al. 1999, 2001; Harvey et al. 2002). In this system, cohort classification is based on the distribution of tree–stem diameters (Bergeron et al. 1999): Cohort 1, consisting of even-aged stands with a high stocking density of small-diameter stems and a unimodal stem-diameter distribution (resulting from clear-cutting and planting to emulate disturbance by fire), Cohort 2, stands with a multi-modal diameter distribution beginning to show uneven age structure (resulting from partial cutting to emulate natural succession), and Cohort 3, inverse-J diameter distribution in stands with both small and large stem diameters, including an established multi-age structure with evident gap dynamics (resulting from selection cutting to emulate natural gap dynamics found in old-growth stands) (Bergeron et al. 1999, 2001). More recent studies have expanded upon the MCM approach to classify stand structure (Kuttner et al. 2013; Latrémouille et al. 2013; Malcolm and Harvey 2013), however, little is known about the potential of MCM to improve upon existing forest management strategies in terms of biodiversity conservation (Etheridge and Kayahara 2013; Malcolm and Harvey 2013). In a recent study, Burrell et al. (2013) showed that four classes of structural variation associated with MCM were relevant in explaining variation among boreal bird communities, but to date, the responses of other faunal communities remains unexplored.

Insects are appropriate ecological models to study the effects of forest management on biological communities, because they are taxonomically and functionally diverse, and have proved to be sensitive to forestry practices (Thiele 1977). There is also mounting evidence that some insect populations worldwide are in decline as a direct result of intensifying management practices in the boreal forest. For example, long-term timber harvesting in Fennoscandia has been linked to simplified forest structure and a resulting loss or extinction of many boreal forest species, including insects (Haila et al. 1994; Niemela et al. 1997). Consequently, insect assemblages are both good ecological models and key conservation taxa to study faunal relationships with forest management in the Nearctic, a forest ecosystem of global significance and where extensive intact, unmanaged areas still remain.

A growing body of literature has examined ground-dwelling insect communities in relation to forest structural variation (e.g., Spence et al. 1996; Vance and Nol 2003; Moore et al. 2004; Work et al. 2004; Buddle et al. 2006). Ground beetles (Coleoptera, Carabidae) are an important group to study because they are ubiquitous, use a wide range of niches related to forest structure, and respond to forest change (Larochelle and Larivière 2003); additionally, their taxonomy is relatively well known, and there is a growing understanding of their ecological requirements. The diversity and abundance of ground beetles tend to be high after clear-cutting, followed by a decline with canopy closure as many open-habitat species are replaced by a smaller set of forest specialists (e.g., Spence et al. 1996; Beaudry et al. 1997; Koivula et al. 2002; Buddle et al. 2006; Niemela et al. 2007). The majority of ground beetles occur across a successional gradient in closed canopy forests, but several rare species are known to be associated specifically with old-growth stands (Niemela et al. 1996). For ground beetle communities, it has been estimated that pre-disturbance conditions are reached after approximately 30 years (Koivula et al. 2002; Vance and Nol 2003; Buddle et al. 2006). However, a study in western Canada showed little evidence of recovery 30 years after harvesting, and in many Fennoscandian forests ground beetles are at low abundances even in relatively old forests due to structural simplification (Niemela et al. 1993; Niemela 1997). Work et al. (2004) found that live crown ratio, basal area (BA) of black spruce trees, high-strata vegetation cover, and plant cover and richness were all associated with carabid abundance in natural stands, while in plantations, ground beetle richness and diversity decreased with increasing canopy cover (Humphrey et al. 1999). In deciduous forest stands, canopy openings created by natural disturbance were also found to reduce carabid species richness, diversity and abundance (Saint-Germain and Mauffette 2001). The small-scale silvicultural techniques proposed in MCM stands may provide enough canopy closure and related forest structures to maintain forest carabids and staphylinids (Koivula et al. 2002; Niemela et al. 2007), but to date, the association between variable forest structure (as could result from MCM) and ground beetles has not been investigated.

Many studies have shown how microclimate and ground-level habitat characteristics such as soil moisture, leaf litter, and downed woody debris (DWD) are relevant for ground beetle populations (e.g., Work et al. 2004; Cobb et al. 2007; Niemela 1997); however, fewer studies have examined the variables related to stem-diameter distributions and multi-cohort characteristics associated specifically with MCM. Given that significant associations have been observed between ground beetles and stand age, canopy cover, tree density, live crown ratio, BA, and vegetation cover (e.g., Niemela et al. 1993; Niemela 1997; Humphrey et al. 1999; Saint-Germain and Mauffette 2001; Koivula et al. 2002; Work et al. 2004; Lange et al. 2014), we predict that the diversity of carabid assemblages will be associated with those variables that are characteristic of MCM stand cohort structure in the Nearctic boreal forest. Our objective was to examine the association between ground beetle community attributes and stand characteristics across different phases (or cohort classes) of stand development. Given that MCM uses the distributions of stem diameters as a key factor to define cohort class, we asked whether parameters associated with live-tree diameter distributions were also relevant for explaining variations in ground beetle community attributes. We compare the performance of these parameters with other traditional habitat variables such as stand age, foliage density in the upper canopy and understory strata, and DWD.

Materials and methods

Study area and design

The study was conducted in northeastern Ontario, Canada, within the northern clay section of the boreal forest (Rowe 1972), a region based on largely lacustrine clay soils with gentle topography and little exposed bedrock. Large stands of black spruce (*Picea mariana* Mill) dominate the landscape, with mixedwood stands of trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* Mill.), and white spruce (*Picea glauca* Voss) found in areas of good drainage (Rowe 1972). Our study sites were selected from those mixedwood stands located within two northern forest management units, Iroquois Falls Forest and Gordon Cosens Forest (average longitude 49° N and latitude −80.6° E) (Kuttner 2006), where forest management began in the early twentieth century (Ontario Ministry of Natural Resources 2009).

In the upland mixedwood forests mentioned above, 18 sites with similar tree species composition were selected to represent a wide range of stand structure and age since disturbance. Mixedwood forest sites were all of type MS2 (as classified by the Ontario Ministry of Natural Resources) and were composed of poplar (*Populus* spp.), white birch, white spruce, black spruce, and balsam fir, such that 21–72 % of stems $\geq$10 cm diameter at breast height (DBH) were deciduous, with all sites having at least some poplar (1–65 %) and spruce (1–61 %; Table 1). Sites ranged from 35 to 130 years since last disturbance and, following Burrell et al. (2013), were classified based on their stem-diameter distribution as either, Cohort Class 1 ($n = 4$), Cohort Class 2 ($n = 3$), Cohort Class 3 ($n = 5$) or Cohort Class 4 ($n = 6$). Stands that were dated prior to when logging began in the region were considered unlogged. All logged stands were clear-cut using horses between 1935 and 1963, except two stands that were mechanically logged in 1964 and 1971. To sample each of the selected sites, a 4 × 4 grid was established at least 50 m from stand edges to avoid edge effects, and with 25 m between sampling stations (covering a 75 × 75 m area) for a total of 16 sampling stations per site. At each sampling station, structural habitat variables were measured and a pitfall trap was set to sample ground beetles.

Insect sampling and identification

Each pitfall trap consisted of two stacked, 11-cm diameter containers with the rim flush to the ground surface; only the inner container was removed when collecting samples to minimize substrate disturbance. Containers were filled partially with a 5 % saline solution and a few drops of unscented detergent to break the surface tension. A plastic lid suspended with nails 3 cm above the trap was used to reduce debris entry. Traps in the 18 sites operated simultaneously and continuously over 1 week in each of June, July, and August of 2007 for a total planned sampling effort of 336 traps/day (16 traps operating over 21 days) at each site. Based on previous studies, our sampling effort was expected to be sufficient for capturing most species in a site (Werner and Raffa 2000). However, abundance of beetles needed to be standardized to account for variation in sampling effort among sites because 18 % of the total traps were lost due to bear predation and other factors. Thus, abundance of beetles was calculated as the number of individuals captured in 100 trap-days. Traps were checked and insects collected at the end of each sampling period and stored for later identification. All collected carabid beetles were identified to species and classified as forest specialist, forest generalist or open habitat species based on recognized taxonomic systems (Lindroth 1961–1969; Larochelle and Larivière 2003).

Multi-cohort characterization

To characterize live-tree diameter distributions, we determined species and DBH for all live stems $\geq$2.5 cm DBH within an area of 6-m radius centered at each beetle sampling station. The two-parameter Weibull probability

Table 1 Characteristics of the 18 sampled mixedwood sites in boreal forests of the central Nearctics, including cohort class, forest age, and percentage composition of tree species by basal area of stems ≥10 cm diameter at breast height

Site names	Cohort classes	Age	%Bp	%Bf	%Wb	%Bs	%Ws	%Ta	%Wi	% Deciduous
KAT1-C1	1	35	1	17	21	5	56	0	0	21
LMW15	1	55	0	7	43	23	7	18	1	62
TEM-01-094	1	50	8	16	20	2	29	22	3	53
TEM-01-101	1	42	8	9	1	12	15	56	0	65
CHAR01	2	59	38	1	26	2	29	4	0	68
KAP00011	2	43	11	29	2	15	21	21	0	34
TEM-03-006	2	71	18	15	2	7	18	37	3	60
ABI-03-14	3	50	0	20	7	21	27	25	0	31
TEM-01-083	3	54	0	49	11	0	19	21	0	32
TEM-01-084	3	54	59	10	13	0	18	0	0	72
TEM-02-098	3	61	41	13	22	0	16	8	0	71
TEM-04-05	3	60	0	38	9	6	11	33	3	45
ABI-02-17	4	130	43	2	4	2	35	15	0	61
ABI-03-10	4	66	0	36	9	1	16	37	0	47
GCF9411	4	110	23	41	17	0	18	0	0	41
LISNC	4	115	0	20	23	3	8	46	0	69
TEM-01-095	4	71	0	6	6	9	15	65	0	71
TEM-03-040	4	44	21	34	26	0	0	18	0	65

Rare tree species (<0.4 % of stems in total) were excluded from percentage basal area calculations

Bp balsam poplar (*Populus balsamifera*), *Bf* balsam fir (*Abies balsamea*), *Wb* white birch (*Betula papyrifera*), *Bs* black spruce (*Picea mariana*), *Ws* white spruce (*Picea glauca*), *Ta* trembling aspen (*Populus tremuloides*), *Wi* willow (*Salix* spp.)

density function was fitted to the stem-diameter distributions, and the parameters (shape [c] and scale [σ]) were used as quantitative descriptors of stand cohort structure. The flexibility of the Weibull distribution allows a variety of tree diameter distributions to be described effectively (e.g., Bailey and Dell 1973; Gove and Patil 1998) with the shape parameter representing the shape of the Weibull probability density function that best fit the dataset (varying from negative exponential to normal), and the scale representing the DBH class at which 63.2 % of the stems were accumulated. Because stems <2.5 cm DBH were not measured, 2.5 for the DBH of all stems was subtracted before fitting the Weibull curves. Given that fine-scale microhabitat features are known to be important for ground beetles, we also investigated community variation as a function of the minimum stem diameter cut off used to characterize stem distributions, i.e., 2.5 versus 10 cm DBH. The Weibull curve parameters were plotted against each other, and cluster analysis was used to identify four site clusters representing four cohorts as follows: Cohort 1, even-aged stands with a high stocking density of small-diameter stems and a unimodal diameter distribution, Cohort 2, stands with a broader diameter distribution, beginning to show uneven age structure, Cohort 3, inverse-J distribution in stands with small diameter stems with some stems belonging to larger diameter classes and with a well-established multi-age structure and evident gap dynamics, and Cohort 4, inverse-J distribution with a sparse tail as stands return to a more homogenous state.

Habitat sampling

At the 6-m radius plots in each site, DBH was measured and BA and percentage composition of deciduous trees by BA (pcdecid) was calculated based on species and DBH; in addition, DBH of snags ≥10-cm diameter was used to calculate the BA of snags (snagBA).

At each site, percentage foliage cover was estimated every 2.5 m along four parallel station transects (of the 4 × 4 beetle sampling stations) spaced 25 m apart and 75 m long. Percentage foliage was sampled by recording a four-point score (0 = 0–10, 1 = 10–50, 2 = 50–75 or 3 = 75–100 %) at different height intervals using a 2.5-m sighting pole. Height intervals were 0–2.5, 2.5–5, 5–10, 10–15, 15–20, 20–25, and 25–30 m, and heights were measured using an optical rangefinder. Based on a principal component analysis (PCA) of site-level means, measurements were correlated within specific height ranges (0–2.5, 2.5–10 and 10–25 m); hence, measurements within them were combined to represent shrub, understory and overstory strata, respectively. Percentage foliage cover was converted to foliage thickness scores (Malcolm 1995), and the mean, variance, and semivariance of foliage thickness for each site were determined for each stratum (meanshr, varshr, svshr, meanund, varund, svund, meanover, varover, svover). The variance provided an overall measure of horizontal heterogeneity; the semi-variance provided a measure of the horizontal grain (or texture) of the variability. Because the variance was correlated with the mean, the mean was partialled out of the variance measurements. Similarly, the mean and variance were partialled out of the semivariance measurements. In addition, we measured the mean, residual variance, and residual semi-variance of canopy heights along transects (meancanh, varcanh, svcanh); in this case, at every measurement point, the canopy height was defined as the midpoint of the highest height interval that had a foliage score of ≥ 1 (if the scores for all intervals were zero for a location, then the canopy height was set to zero for that location). Vertical foliage complexity was determined using the Shannon diversity index (vert_H) based on the foliage thickness scores in the seven height intervals. At each of the 16 grid intersections, shrub openness was measured in four directions (N, S, E, W). A 2-m length pole, marked in 10-cm segments, was held 5 m away from the observer, and the number of segments completely unobstructed by foliage, twigs or DWD was recorded. The mean of the four measurements per intersection was calculated, and then a mean shrub openness (shrubopen) value was estimated per site.

Measurements of foliage, and diameter (≥ 7 cm) and decay class (using classes 1–5 by Hayden et al. 1995) of DWD were made at the point where the DWD intersected the transect along each of the four 75-m transects. Volume was calculated using Van Wagner's (1968) formula for each decay class; volumes were subsequently calculated for just two decay classes (new = decay classes 1 and 2, and old = decay classes 3–5).

Age since last disturbance was obtained from forest resource inventory data. Vegetation type was determined using Ontario's northeast Forest Ecosystem Classification (FEC) at the four corners of the grid and at one station in the center. Vegetation types were ranked according to the number of herb species, and a weighted average of ranks was calculated for each site. Because vegetation types in FEC have been suggested as a correlate of overall site productivity (Sharkey 2008), vegetation types were ranked according to the number of herb species, and a weighted average of ranks was calculated as a measure of productivity for each site.

Statistical analysis

To analyze associations between species abundances and stand characteristics, we first examined underlying gradients in ground beetle communities among the sites using PCA on the correlation matrix of log-transformed species abundances. Structural variables were plotted passively and only those variables with relatively high scores (≥ 0.40 on either axis) were shown. We tested significance of the Weibull parameters for live stems ≥ 2.5 cm DBH (termed "all stems") and for stems ≥ 10 cm (referred to as "trees"). As the next step, we used permutations of redundancy analyses (RDAs) to test the significance of each structural variable individually and, via forward selection, of them in combination (9999 permutations per test). We also tested significance of the Weibull parameters for live stems >2.5 cm DBH (termed "all stems") and for stems >10 cm (termed "trees"). To test whether Weibull shape or scale explained the greatest amount of variation in the carabid matrix, we used forward selection (9999 Monte Carlo permutations). RDA on the ground beetle correlation matrix was also conducted using cohort class (coded as dummy variables), again with Monte Carlo tests of significance. We also conducted univariate tests to examine differences in species abundances among cohort classes. For Carabidae species found in more than one-third of the sites, we used a one-way ANOVA on log-transformed data (except for *Sphaeroderus nitidicollis*, for which transformation was not required). One common species, *Synuchus impunctatus* still violated assumptions of normality and homogeneity; hence a median test was used. All species found in less than one-third of the sites were tested using median tests.

To examine community attribute–stand characteristic associations, we analyzed correlations between habitat variables and ground beetle total abundance, species richness, and diversity using a simple rarefaction technique to allow comparisons of species richness of samples with different beetle abundance; specifically, the number of species found in each site was plotted against the number of individuals captured, and residuals from a semi-logarithmic curve fitted to the data were used as corrected richness values. Diversity was measured using the Shannon–Weiner index (H′). Community metrics were explored using PCA on the correlation matrix, with all habitat variables plotted passively. RDA was used to test for significance of the structural variables (9999 Monte Carlo permutations). Differences in community metrics among cohort classes were examined with ANOVA tests. Examinations of residuals indicated that assumptions of normality and homogeneity were justified. All multivariate tests were undertaken with CANOCO for Windows (v. 4.5); univariate tests were run with SAS (v. 9.1).

To compare the predictive power of Weibull parameters describing stem-diameter distribution with other habitat variables, we used partial canonical correspondence analysis (PCCA). This test determined whether structural variables had significant explanatory power alone and after other variables (such as Weibull parameters) were considered. The performance of Weibull parameters was compared against eight sets of habitat measures determined a priori: (1) canopy height (mean, variance, semi-variance), (2) understory foliage thickness (mean, variance, semi-variance of understory foliage thickness), (3) shrub openness, (4) vertical foliage complexity, (5) DWD (BA of snags, both early-decay and late-decay DWD volume), (6) stand age, (7) productivity, and (8) percentage deciduous composition.

Results

Overall, 2092 individual ground beetles, representing 25 species, were captured in pitfall traps (Table 2). Of the total number of individuals, 72 % belonged to four species: *Platynus decentis* (27 %), *Pterostichus adstrictus* (23 %), *Pterostichus coracinus* (15 %) and *Pterostichus pensylvanicus* (8 %). The following species were rarely found: *Loricera pilicornis* (Cohort 1), *Carabus granulatus* (Cohort 2), *Platynus mannerheimi* (Cohorts 1 and 2), and *Trechus apicalis*, and *Harpalus somnulentus* (Cohort 3).

Species abundance–stand characteristic associations

The PCA on the correlation matrix of ground beetle abundances showed two main patterns of correlation (Fig. 1). Sites in the upper right quadrat (Cohort 2 sites; $P = 0.005$) had high understory grain (semi-variance of understory foliage thickness; $P = 0.007$), high shrub openness ($P = 0.037$), and high values of the Weibull parameters for all stems ($P = 0.050$ and 0.011 for shape and scale, respectively). The remaining cohort classes had relatively low values for these variables and showed little evidence of separation by cohort class. Species positively associated with the first axis included: *P. coracinus*, *Carabus nemoralis*, *C. granulatus*, *Pterostichus melanarius*, *S. impunctatus*, and *P. decentis*; a weak negative association was shown by *Agonum retractum*. *P. melanarius* and *C. nemoralis* are both non-native species and were associated with Cohort 2 stands. The second axis of correlation reflected variation among non-Cohort 2 sites. Sites in the lower right quadrat had high canopy height variability ($P = 0.023$). Species positively associated with this axis included: *Sphaeroderus stenostomus*, *Scaphinotus bilobus*, *S. nitidicollis*, and *P. pensylvanicus*; negative associates included *Calathus ingratus*, *Pterostichus punctissimus*, *H. somnulentus*, *T. apicalis* and *P. adstrictus*. When all variables were subjected to forward selection, in addition to understory grain, significant variables were the residual variance of canopy height ($P = 0.016$) and the Cohort 2 dummy variable ($P = 0.039$). Univariate tests on cohort class were not significant for any of the species caught at four or more sites, except for *P.* (*Batenus*) *mannerheimi*, which was caught only in stands from Cohort Class 2 (Table 2).

Community attribute–stand characteristic associations

In general, the PCA bi-plot of community attributes (Fig. 2) showed a similar pattern to that found for species abundances (Fig. 1). Sites in the top right quadrant tended to be Cohort 2 sites ($P = 0.023$) and were characterized by high total abundance and by relatively high shape ($P = 0.046$) of all stem-related Weibull parameters. Canopy height also tended to be high on average for these sites. Sites in the lower right quadrant were characterized by diverse ground beetle communities (high H'), in that, as in Fig. 1, they had high variability in canopy height ($P = 0.018$) and also high variability in the overstory ($P = 0.018$). Both of these sets of sites, in comparison to the left on the first axis, had high species richness, which was associated with a fine-grained understory ($P = 0.0191$) and, to a lesser extent, with a fine-grained canopy and a relatively high deciduous BA component. When all variables were subjected to forward selection, in addition to variability of canopy height, only fine-grained understory was significant ($P = 0.012$). ANOVAs showed that total abundance ($F = 3.09$, $P = 0.063$), richness ($F = 0.51$, $P = 0.679$), and diversity ($F = 0.89$, $P = 0.471$) did not differ significantly among cohort classes.

Predictive power of Weibull parameters

Weibull parameters of live tree stems ≥2.5 cm DBH were better predictors of ground beetle communities than parameters of tree stems ≥10 cm DBH; consequently, we used the former in variance decomposition analyses. Weibull parameters for stand structure were the strongest predictors of ground beetle communities compared with more traditional habitat variables (Table 3); however, vertical foliage complexity, understory thickness, and percentage deciduous composition were also significant. All other variables were not significant, including canopy height, shrub openness, DWD, age, and productivity (Table 3). For most non-significant variables (DWD, age, and productivity), the unique contribution of Weibull parameters was significant. The exception was shrub openness, for which the unique contribution of Weibull parameters was not significant. For habitat variables that were significant, the unique contribution of Weibull parameters was no longer significant. Vertical foliage complexity showed a similar relationship (although corresponding P values were 0.070 and 0.106), supporting the pattern shown in the ordination (Fig. 1): a secondary axis

Table 2 Mean abundances of ground beetle species (number of individuals per 100 trap-days) in structural cohort classes in boreal forests of the central Nearctic

Species	Cohort class[a]				Overall mean abundance	Univariate tests[b] (C/F, *P*)
	1 (*n* = 4)	2 (*n* = 3)	3 (*n* = 5)	4 (*n* = 6)		
Forest specialists						
Calosoma (*Calosoma*) *frigidum* Kirby	0	0	0.424	0.149	0.167	C = 3.17, *P* = 0.366
Sphaeroderus nitidicollis brevoorti LeConte	1.244	1.412	0.968	1.638	1.326	F = 0.25, *P* = 0.861
Sphaeroderus stenostomus lecontei Dejean	0.476	1.573	1.403	0.914	1.062	C = 1.25, *P* = 0.740
Agonum retractum LeConte	0.192	0.247	0.668	0.455	0.421	F = 1.61, *P* = 0.231
Pterostichus (*Bothriopterus*) *pensylvanicus* LeConte	8.205 (1.416)	4.155	1.800	3.195	4.081	F = 0.34, *P* = 0.798
Mean	2.368 (0.989)	1.921	2.254	2.089	2.169	
Forest generalists						
Carabus (*Archicarabus*) *nemoralis* Müller	0	1.786	0	0	0.298	C = 5.00, *P* = 0.172
Scaphinotus (*Nomaretus*) *bilobus* (Say)	1.116	1.888	1.782	1.868	1.680	C = 1.45, *P* = 0.694
Harpalus (*Euharpalops*) *fulvilabris* Mannerheim	0.223	0	0	0.549	0.233	C = 4.25, *P* = 0.235
Calathus ingratus Dejean	4.975	1.326	0.974	1.495	2.095	F = 0.88, *P* = 0.477
Platynus (*Platynus*) *decentis* (Say)	11.337	28.571	16.805	13.936	165.95	F = 1.28, *P* = 0.318
Synuchus (*Pristodactyla*) *impunctatus* (Say)	2.809	7.565	7.706	2.004	4.694	C = 5.17, *P* = 0.160
Pterostichus (*Bothriopterus*) *adstrictus* Eschscholtz	13.365	11.546	9.878	4.890	9.268	F = 1.39, *P* = 0.287
Pterostichus (*Euferonia*) *coracinus* (Newman)	3.593	34.008	5.190	3.932	9.219	F = 0.75, *P* = 0.539
Pterostichus (*Lenapterus*) *punctissimus* (Randall)	2.714	0.935	0.902	1.432	1.487	C = 1.91, *P* = 0.591
Pterostichus (*Morphnosoma*) *melanarius* (Illiger)	0	3.982	0.204	0	0.720	C = 7.03, *P* = 0.071
Trechus apicalis Motschulsky	0	0	0.260	0	0.072	C = 2.60, *P* = 0.457
Mean	3.628	8.328	3.973	3.025	4.215	
Open-habitat species						
Harpalus somnulentus Dejean	0	0	0.408	0	0.113	C = 2.60, *P* = 0.457
Hygrophilous species						
Carabus granulatus granulatus Linné	0	0.298	0	0	0.050	C = 5.00, *P* = 0.172
Loricera pilicornis pilicornis (Fabricius)	0.325	0	0	0	0.072	C = 3.50, *P* = 0.321
Platynus (*Batenus*) *mannerheimi* (Dejean)	0	1.318	0	0	0.220	**C = 10.62, *P* = 0.014**
Mean	0.108	0.538	0.065	0	0.114	
Harpalus species	0.275	0	0	0	0.061	C = 3.50, *P* = 0.321
Total mean abundance	2.493	4.897	2.637	1.938	2.749	

Statistically significant values are bolded

[a] Numbers in parenthesis are when one site with extremely high abundance was excluded. Site was not excluded for overall tests as only one species showed this trend

[b] Statistics and *P* values from univariate tests of cohort effects. F values (degrees of freedom = 3) are from ANOVAs, χ^2 values (C) are from a median test

of variation nearly orthogonal to the all-stem Weibull parameters was correlated with canopy height variables and vertical foliage complexity.

Discussion

Weibull parameters from the diameter distribution of all stems were better predictors of ground beetle abundance and community attributes than any other habitat variables measured in this study. Similar results were found when analyzing boreal bird community responses to multi-cohort related structural variation in boreal mixedwood forests (Burrell et al. 2013). This predictive power appears to be related primarily to the scale parameter, which in turn was correlated with the grain of the understory vegetation, canopy height, and shrub openness. The shape parameter provided less explanatory power. Cohort class, which was defined based on both parameters, was of relatively little value in predicting variation of the beetle communities. Instead, we found evidence of a second axis of variation related to canopy height variability that was independent of the Weibull all-stem parameters. Richness of ground beetle communities seemed to be the highest when high and

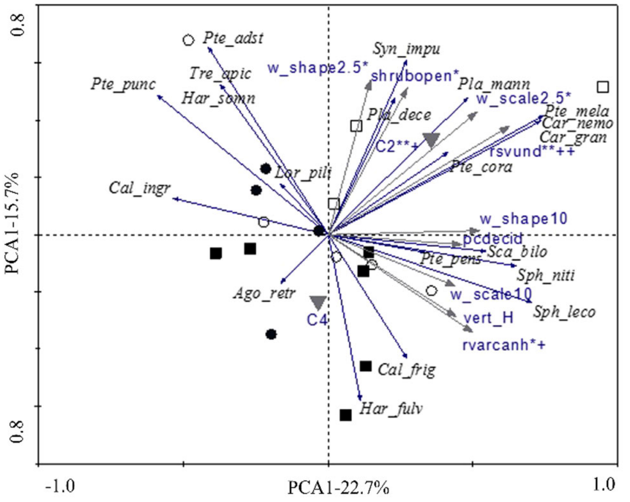

Fig. 1 Principal components analysis on the correlation matrix of ground beetle abundances from pitfall trapping conducted in Nearctic boreal forest stands of different cohorts. Environmental variables are plotted passively; acronyms are in the text (only those variables with *axis* scores ≥0.40 shown). Significance of each variable is shown (**$P \leq 0.01$, *$P \leq 0.05$, $^{++}P < 0.01$ in forward selection, $^{+}P < 0.05$ in forward selection). Site *symbols* represent classes of multi-cohort forest structure (*filled circles* Cohort 1, *open squares* Cohort 2, *open circles* Cohort 3, *filled squares* Cohort 4). See text for more details

heterogeneous canopies were accompanied by finely-dissected horizontal variability in the understory. In forest stands across Germany, the effects of forest type on ground beetle community attributes were mainly mediated by structural habitat parameters such as canopy cover and plant diversity (Lange et al. 2014).

Presumably, canopy height variability and associated fine-grained understories are associated with fine-scale variation in conditions close to the ground. Microclimate and ground-level features have been found to be important for forest-dwelling carabids (Work et al. 2004; Lassau et al. 2005; Cobb et al. 2007). Niemela et al. (1996) showed that it is possible to have high species turnover due to high microsite variation even in small areas that may not appear to be structurally developed at a stand scale. Of course, at a larger-scale, structural variables can also dictate microclimate conditions (Werner and Raffa 2000; Work et al. 2004), and the pattern we observed may have reflected gap phase dynamics (Klimaszewski et al. 2005). For example, canopy closure and associated changes in the understory can play a key role in assemblage formation because they affect relevant microclimatic factors such as soil moisture and temperature (Niemela et al. 1993, Spence et al. 1996; Lassau et al. 2005; Buddle et al. 2006).

We did not find stand age to be a strong correlate of ground beetle community composition compared to the Weibull parameters and overstory and understory structural features. Many studies on ground beetle habitat have focused on time since disturbance (=age) as a key variable because carabid diversity, abundance, and richness has been consistently shown to be associated with young stands that change over time with stand chronology, i.e., from communities dominated by open-habitat species to those characterized by forest specialists (Beaudry et al. 1997; Koivula et al. 2002; Klimaszewski et al. 2005; Niemela et al. 2007). However, the literature is conflicting on this in that other studies have found community changes along an age gradient to be less apparent following the closure of stand canopies (Paquin 2008; Buddle et al. 2006), and this may account for the low relevance of age in our study compared to structural features. All of the stands in our study had closed canopies and ranged in age from 35 to 130 years. Our results support the idea that in such closed-canopy forests, time since disturbance is not a useful variable for classifying cohort-related structural variability and its associated wildlife communities, presumably because of inherent variability in site characteristics and secondary disturbances that influence stand structure after the initial disturbance, especially at the microhabitat scale (Harvey et al. 2002).

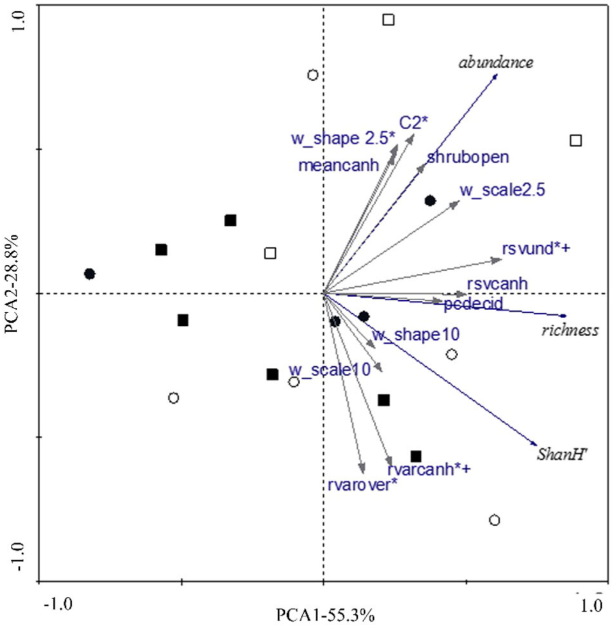

Fig. 2 Principal components analysis on ground beetle abundance, diversity (H′), and richness estimated from pitfall trapping conducted in Nearctic boreal forest stands of different cohorts. Environmental variables are plotted passively; acronyms are in the text (only those variables with *axis* scores ≥0.40 shown). Significance of each variable is shown (**$P \leq 0.01$, *$P \leq 0.05$, $^{++}P < 0.01$ in forward selection, $^{+}P < 0.05$ in forward selection). Site *symbols* represent classes of multi-cohort forest structure (*filled circles* Cohort 1, *open squares* Cohort 2, *open circles* Cohort 3, *filled squares* Cohort 4). See text for details

Table 3 Partial canonical correspondence analysis examining the relative value of various habitat predictors in comparison to Weibull parameters from the diameter distribution of stems ≥2.5 cm DBH in explaining ground beetle community composition from pitfall traps in boreal forests of the central Nearctic

Habitat variables	Source of variation	% Var	*P* value
Weibull parameters	**Weibull**	**18.6**	**0.007**
Canopy height	**Together**	**40.0**	**0.003**
	Canopy height	22.4	0.087
	Unique to Weibull	**17.6**	**0.010**
	Unique to canopy height	21.4	0.051
	Shared	1.0	
Understory foliage thickness	**Together**	**37.5**	**0.042**
	Understory foliage thickness	**24.9**	**0.042**
	Unique to Weibull	12.6	0.246
	Unique to understory foliage thickness	18.9	0.211
	Shared	6.0	
Shrub openness	Together	22.4	0.074
	Shrub openness	7.4	0.230
	Unique to Weibull	14.9	0.110
	Unique to shrub openness	3.8	0.807
	Shared	3.7	
Downed woody debris	Together	33.7	0.157
	Downed woody debris	16.3	0.622
	Unique to Weibull	**17.4**	**0.048**
	Unique to downed woody debris	15.1	0.622
	Shared	1.2	
Vertical foliage diversity	**Together**	**26.2**	**0.004**
	Vertical foliage diversity	**11.0**	**0.013**
	Unique to Weibull	**15.2**	**0.070**
	Unique to vertical foliage diversity	7.6	0.106
	Shared	3.2	
Age	Together	22.1	0.087
	Age	4.1	0.770
	Unique to Weibull	**18.0**	**0.022**
	Unique to age	3.5	0.846
	Shared	0.6	
Productivity	**Together**	**24.1**	**0.041**
	Canopy productivity	7.1	0.289
	Unique to Weibull	**17.0**	**0.035**
	Unique to productivity	5.5	0.406
	Shared	1.6	
% Deciduous composition	**Together**	**24.6**	**0.017**
	% Deciduous composition	**10.1**	**0.025**
	Unique to Weibull	14.5	0.103
	Unique to % deciduous composition	6.1	0.328
	Shared	4.1	

Statistically significant values are bolded

Surprisingly, we found little evidence that DWD quality and quantity were strong predictors of ground beetle communities. Although DWD is often found to be important for ground-dwelling fauna (Work et al. 2004; Cobb et al. 2007), in some cases, such as stands of mature mixedwoods, only weak associations between DWD and wildlife communities have been observed. In their study with carabids, Pearce et al. (2003) found DWD to be more relevant in clear-cut areas than in closed forests, perhaps because DWD was not a limiting factor in the mature forest sites. Similarly, Vanderwel et al. (2009) found evidence that late-decay DWD was relevant for small mammals, but only when available in short supply.

There was a strong correlation between the abundances of several forest specialists (*S. stenostomus*, *S. nitidicollis*, *Calosoma frigidum* and *P. pensylvanicus*) and variability in canopy height, as well as presence of large trees and high vertical foliage complexity. These structures are typically associated with mature stands that have well-developed structure and are undergoing gap phase dynamics, favourable for forest specialists. For example, *P. pensylvanicus* is considered a ubiquitous forest specialist associated with DWD used for over-wintering sites (Larochelle and Larivière 2003; Work et al. 2004; Klimaszewski et al. 2005). Another forest specialist, *C. frigidum*, has been noted to be most abundant in undisturbed mature forest with thick leaf litter (Beaudry et al. 1997; Larochelle and Larivière 2003). *H. somnulentus* is known as an open-habitat species, and it showed a negative association with mature forest features in our ordination. Forest generalists, on the other hand, were associated with several different axes. For example, *C. nemoralis* and *P. melanarius* were associated with the grain of understory thickness, and are both known to use a range of forest habitat structures potentially supported by a fine-grained understory (Werner and Raffa 2000; Larochelle and Larivière 2003; Klimaszewski et al. 2005). Other forest generalists, such as *P. punctissimus*, *P. adstrictus* and *C. ingratus*, were negatively associated with variability in canopy height, suggesting that they may be more abundant in young, less developed forest stands (Niemela et al. 1993; Klimaszewski et al. 2005.

We found the non-native species, *P. melanarius* and *C. nemoralis*, associated with our Cohort 2 stands; both of these species have been linked to anthropogenic habitats (Lindroth 1961–1969; Werner and Raffa 2000; Larochelle and Larivière 2003). The latter species is flightless and can also inhabit mixedwood forests (Larochelle and Larivière 2003); this, plus its limited ability to disperse may explain why it was found in the two stands closest to a town (Kapuskasing). The other exotic species, *P. melanarius*, was found not only in the three Cohort 2 sites but also in Cohort 3 and 4 sites, all further from town, and this perhaps reflects its greater dispersal abilities and wide range of habitats used (Lindroth 1961–1969; Niemela and Spence 1991; Larochelle and Larivière 2003).

Our community metric ordination was similar to that based on the overall species abundance matrix. Sites with diverse carabid communities had high variability in the canopy and were able to support forest specialists in addition to forest generalists (Koivula et al. 2002). Our Cohort 2 sites, which had begun to show uneven age structure, had higher ground beetle abundances, in part due to their association with the forest generalists *P. decentis* and *S. impunctatus*; both were amongst the most numerous species collected. Richness was positively associated with fine-grained understories and variable canopies, showing the importance of spatial heterogeneity in maintaining rich communities. Heterogeneity provides a wide range of ecological niches, promoting diverse assemblages (Klimaszewski et al. 2005). The fact that the majority of ground beetle species we found occurred across a structural gradient (as also observed by Niemela et al. 1996), indicates that a range of cohort classes in the boreal landscape allows species to persist (through immigration and/or reproduction) in patches of variable structure.

Our results provide evidence that the mosaic of differently-structured stands, similar to that arising from MCM, may retain a natural range of ground beetle species across the boreal forest, even though such managed stands might be younger than unlogged, old-growth stands. For example, selection cutting after one rotation in northern deciduous forests seemed to have few long-term effects on ground beetles (Vance and Nol 2003), and small-gap harvesting was able to sustain forest carabid communities similar to those found in mature stands (Klimaszewski et al. 2005). Nevertheless, the loss of the most vulnerable old-growth carabid species remains of concern in forest management operations. MCM was developed to better address the natural disturbance regime of boreal forests by managing simultaneously for both even-age and multi-age stands, and has the potential to provide a diverse array of stand structures that better emulate the natural mosaic (Bergeron et al. 1999). Further research is needed to examine the effects of selection and partial cutting in the boreal context, and the extent to which such practices can maintain, or even restore, the rare species and biological communities of natural multi-cohort forests.

Acknowledgments The authors thank K. Ryan, C. Sharkey, B. Kuttner, M. Burrell, C. Darling, P. de Groot, N. Islam, H. Goulet, D. Swinson, D. Kearns, D. Maguire, and N. Revinskaya for their assistance. Funding was provided by the Forestry Futures Trust, Tembec, Inc., Lake Abitibi Model Forest, Ontario Ministry of Natural Resources, National Science and Engineering Research Council of Canada, and the University of Toronto.

References

Attiwill PM (1994) The disturbance of forest ecosystems—the ecological basis for conservative management. For Ecol Manag 63:247–300

Bailey RL, Dell TR (1973) Quantifying diameter distributions with the Weibull function. For Sci 19:97–104

Beaudry S, Duchesne LC, Cote B (1997) Short-term effects of three forestry practices on carabid assemblages in a jack pine forest. Can J For Res 27:2065–2071

Bergeron Y, Harvey B (1997) Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixedwood forest of Quebec. For Ecol Manag 92:235–242

Bergeron Y, Harvey B, Leduc A, Gauthier S (1999) Forest management guidelines based on natural disturbance dynamics: stand and forest-level considerations. For Chron 75:49–54

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, Drapeau P, Gauthier S, Lecomte N (2007) Using knowledge of natural disturbances to support sustainable forest management in the northern Clay Belt. For Chron 83:326–337

Buddle CM, Langor DW, Pohl GR, Spence JR (2006) Arthropod responses to harvesting and wildfire: implications for emulation of natural disturbance in forest management. Biol Conserv 128:346–357

Burrell MVA, Malcolm JR, Drapeau P (2013) Multi-cohort stand structure as a coarse filter of variation in mixedwood boreal bird communities. For Chron 89:327–339

Cobb TP, Langor DW, Spence JR (2007) Biodiversity and multiple disturbances: boreal forest ground beetle (Coleoptera: Carabidae) responses to wildfire, harvesting, and herbicide. Can J For Res 37:1310–1323

Etheridge DA, Kayahara GJ (2013) Challenges and implications of incorporating multi-cohort management in northeastern Ontario, Canada: a case study. For Chron 89:315–326

Gove JH, Patil GP (1998) Modeling the basal area-size distribution of forest stands: a compatible approach. For Sci 44:285–297

Haila Y, Hanski IK, Niemela J, Punttila P, Raivio S, Tukia H (1994) Forestry and the boreal fauna—matching management with natural forest dynamics. Ann Zool Fenn 31:187–202

Harvey BD, Leduc A, Gauthier S, Bergeron Y (2002) Stand-landscape integration in natural disturbance-based management of the southern boreal forest. For Ecol Manag 155:369–385

Hayden J, Kerley J, Carr D, Kenedi T, Hallarn J (1995) Ontario forest growth and yield program field manual for establishing and measuring permanent sample plots. Ontario Ministry of Natural Resources, Ontario Forest Research Institute, Sault Ste. Marie

Humphrey JW, Hawes C, Peace AJ, Ferris-Kaan R, Jukes MR (1999) Relationships between insect diversity and habitat characteristics in plantation forests. For Ecol Manag 113:11–21

Klimaszewski J, Langor DW, Work TT, Pelletier G, Hammond HEJ, Germain C (2005) The effects of patch harvesting and site preparation on ground beetles (Coleoptera, Carabidae) in yellow birch dominated forests of southeastern Quebec. Can J For Res 35:2616–2628

Koivula M, Kukkonen J, Niemela J (2002) Boreal carabid-beetle (Coleoptera, Carabidae) assemblages along the clear-cut originated succession gradient. Biodivers Conserv 11:1269–1288

Kuttner BG (2006) Description, characterization and identification of stand structure classes in northeastern Ontario: the application of multi-cohort concepts in the classification of stands from four forest types to cohorts. Technical Report No. 3, Lake Abitibi Model Forest, Ontario

Kuttner BG, Malcolm JR, Smith SM (2013) Multi-cohort stand structure in boreal forests of northeastern Ontario: relationships with forest age, disturbance history, and deadwood features. For Chron 89:290–303

Lange M, Türke M, Pašalic E, Boch S, Hessenmöller D, Müller J, Prati D, Socher SA, Fischer M, Weisser WW, Gossner MM (2014) Effects of forest management on ground-dwelling beetles (Coleoptera; Carabidae, Staphylinidae) in Central Europe are mainly mediated by changes in forest structure. For Ecol Manag 329:166–176

Larochelle A, Larivière MC (2003) A natural history of the ground-beetles (Coleoptera: Carabidae) of America north of Mexico. Pensoft Publishers, Sophia

Lassau SA, Hochuli DF, Cassis G, Reid CAM (2005) Effects of habitat complexity on forest beetle diversity: Do functional groups respond consistently? Divers Distrib 11:73–82

Latrémouille C, Valeria O, Harvey BD (2013) Historical analysis of landscape change in the eastern boreal mixedwood: a case study in the context of cohort-based management. For Chron 89:304–314

Lindroth CH (1961–1969) The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska, Parts 1–6. Opuscula Entomologica Supplementa 20, 24, 29, 33, 34, 35, Lund

Malcolm JR (1995) Forest structure and the abundance and diversity of neotropical small mammals. In: Lowman MD, Nadkarni NM (eds) Forest canopies. Academic, San Diego, pp 179–197

Malcolm JR, Harvey BD (2013) The need for multi-cohort management in boreal forests. For Chron 89:271–274

Moore JD, Ouimet R, Houle D, Camire C (2004) Effects of two silvicultural practices on ground beetles (Coleoptera: Carabidae) in a northern hardwood forest, Quebec, Canada. Can J For Res 34:959–968

Niemela J (1997) Invertebrates and boreal forest management. Conserv Biol 11:601–610

Niemela J, Spence JR (1991) Distribution and abundance of an exotic ground-beetle (Carabidae)—a test of community impact. Oikos 62:351–359

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

Niemela J, Haila Y, Punttila P (1996) The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. Ecography 19:352–368

Niemela J, Spence JR, Carcamo H (1997) Establishment and interactions of carabid populations: an experiment with native and introduced species. Ecography 20:643–652

Niemela J, Koivula M, Kotze DJ (2007) The effects of forestry on carabid beetles (Coleoptera: Carabidae) in boreal forests. J Insect Conserv 11:5–18

Ontario Ministry of Natural Resources (2009) List of forest management units. OMNR website. http://www.mnr.gov.on.ca/en/Business/Forests/1ColumnSubPage/STEL02_163535.html. Accessed 15 Jan 2009

Paquin P (2008) Carabid beetle (Coleoptera: Carabidae) diversity in the black spruce succession of eastern Canada. Biol Conserv 141:261–275

Pearce J, Venier LA, Mckee J, Pedlar J, Mckenney D (2003) Influence of habitat and microhabitat on carabid (Coleoptera: Carabidae) assemblages in four stand types. Can Entomol 135:337–357

Rowe JS (1972) Forest regions of Canada. Revised edition. Department of the Environment, Canadian Forestry Service, Publication No. 1300. Information Canada, Ottawa, p 172

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

Sharkey CA (2008) Small mammal communities and multicohort stand structure in boreal northeastern Ontario. MScF Thesis, Faculty of Forestry, University of Toronto

Spence JR, Langor DW, Niemela J, Carcamo HA, Currie CR (1996) Northern forestry and carabids: the case for concern about old-growth species. Ann Zool Fenn 33:173–184

Thiele HU (1977) Carabid beetles in their environments: a study on habitat selection by adaptations in physiology and behaviour. In: Zoophysiology and ecology, vol 10. Springer, Berlin

Van Wagner CE (1968) The line intercept method in forest fuel sampling. For Sci 14:20–26

Vance CC, Nol E (2003) Temporal effects of selection logging on ground beetle communities in northern hardwood forests of eastern Canada. Ecoscience 10:49–56

Vanderwel MC, Mills SC, Malcolm JR (2009) Effects of partial harvesting on vertebrate species associated with late-successional forests in Ontario's boreal region. For Chron 85:91–104

Werner SM, Raffa KF (2000) Effects of forest management practices on the diversity of ground-occurring beetles in mixed northern hardwood forests of the Great Lakes region. For Ecol Manag 139:135–155

Work TT, Shorthouse DP, Spence JR, Volney WJA, Langor D (2004) Stand composition and structure of the boreal mixedwood and epigaeic arthropods of the Ecosystem Management Emulating Natural Disturbance (EMEND) landbase in northwestern Alberta. Can J For Res 34:417–430