Evaluation of carabid beetles as indicators of forest change in Canada[1]

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Abstract—Our objective was to assess the potential of carabid beetles (Coleoptera: Carabidae) as effective bioindicators of the effects of forest management at a Canadian national scale. We present a comparison of carabid beetle assemblages reported from large-scale studies across Canada. Based on the initial response following disturbance treatment, we found that carabid assemblages consistently responded to disturbance, but responses of individual species and changes in species composition were nested within the context of regional geography and finer scale differences among forest ecosystems. We also explored the relationship between rare and dominant taxa and species characteristics as they relate to dispersal capacity and use of within-stand habitat features such as coarse woody debris. We found no relationship between life-history characteristics (such as body size, wing morphology, or reported associations with downed wood) and the relative abundance or frequency of occurrence of species. Our results suggest that carabids are better suited to finer scale evaluations of the effects of forest management than to regional or national monitoring programs. We also discuss several knowledge gaps that currently limit the full potential of using carabids as bioindicators.

Résumé—Notre objectif est d'évaluer l'efficacité potentielle des carabes (Coleoptera: Carabidae) comme bioindicateurs des effets de l'aménagement forestier à l'échelle canadienne. Nous comparons les peuplements de carabidés dans des études de grande envergure faites dans diverses régions canadiennes. D'après leur réaction initiale à la perturbation, les peuplements de carabes

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Received 16 April 2006. Accepted 24 January 2007.

[1] Presented as part of the symposium "Maintaining Arthropods in Northern Forest Ecosystems" at the Joint Annual Meeting of the Entomological Societies of Canada and Alberta, 4 November 2005, Canmore, Alberta.

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Can. Entomol. **140**: 393–414 (2008)

répondent de façon cohérente aux effets des perturbations, bien que les réactions des espèces individuelles et les changements de composition spécifique soient emboîtés dans le contexte de la géographie régionale et des différences fines entre les écosystèmes forestiers. Nous examinons aussi les relations entre les espèces rares et dominantes, de même que les caractéristiques des espèces, en ce qui a trait à la capacité de dispersion des espèces et des particularités des habitats au sein des peuplements forestiers, comme la présence de débris ligneux grossiers. Il n'existe pas de relation entre les caractéristiques biologiques des carabes (telles que la taille corporelle, la morphologie alaire ou l'association présumée avec le bois mort au sol) et l'abondance relative ou la fréquence des espèces. Nos résultats indiquent que les carabes peuvent mieux servir aux évaluations fines des effets des aménagements forestiers qu'aux programmes de surveillance à l'échelle régionale ou nationale. La discussion traite de plusieurs lacunes dans nos connaissances qui restreignent la pleine utilisation potentielle des carabes comme bioindicateurs.

[Traduit par la Rédaction]

Introduction

The use of indicator species to evaluate effects of anthropogenic and natural disturbances in forests has been suggested as an important and realistic tool for defining sustainable forest management in Canada and elsewhere (Lindenmayer *et al*. 2000). In some cases, policy objectives have emphasized the use of species that are vulnerable or in other ways sensitive to changing forest conditions as ecological indicators (Canadian Council of Forest Ministers 2003). Because of a litany of factors (ranging from species-specific concerns to a more fundamental lack of basic inventory data), species that can and should be included in biodiversity monitoring programs and the way in which management strategies will be changed as a result of biomonitoring activities remain largely undetermined. Although the concept of biodiversity "indicators" is central to many published discussions of sustainable forest management, there are few robust examples of its practical application.

In this context the use of bioindicators has been extended to evaluate nebulous qualities like "ecosystem health" that cannot be easily or directly measured. Although the concept of ecosystem health seems straightforward, strategies aimed at achieving this goal may fail because of our inability to distinguish healthy ecosystems from those reasonably classified as unhealthy. Even the criterion of adherence to a contemporary standard of biotic structure is inadequate because biological systems are dynamic and we expect processes such as climate change to alter them dramatically.

Any species or higher taxon that is sensitive to environmental change has potential as an indicator. At least three broad criteria are central to the development of effective indicators (McGeoch 1998). (1) The best indicators will consistently respond monotonically over the entire range of disturbance and scale of expected change. Clearly, the effectiveness of potential indicators should be evaluated through rigorous experimental studies before they are considered to be effective tools for conservation or forest-management planning. (2) Realistic estimations of costs and benefits of using a particular indicator must also be evaluated when designing effective monitoring strategies. There are often substantial "hidden" costs in addition to the costs of collecting samples, including sorting of specimens, making species-level identifications, maintaining working databases that adequately store information, and access to taxonomic expertise for particular groups of indicators. (3) Finally, effective use of taxon-based indicators to evaluate the impact of disturbances, such as those associated with forest management, requires monitoring designs to be rigorous enough to allow changes in indicators to be compared with reasonable and adequate control conditions such as uncut forest stands or reserves. Absence of clear controls leaves us highly uncertain that biodiversity changes are indeed associated with the disturbances of concern. Meeting these criteria requires careful consideration of the biology of potential indicator taxa, including life-history traits, capacity for dispersal, and potential interactions with other species.

Carabid beetles (Coleoptera: Carabidae) have received considerable attention as potential biodindicators of the effects of disturbance in northern forests (Niemela 2001; Rainio and Niemela 2003). They have been used to reflect forest habitat changes associated with a variety of management conditions including specific harvesting practices, such as clear-cutting (Niemela *et al.* 1993; Abildsnes and Tommeras 2000; Werner and Raffa 2000; Heliola *et al.* 2001; Koivula *et al.* 2002), partial-cut harvesting or thinning (Lemieux and Lindgren 2004; Moore *et al.* 2004; Peck and Niwa 2004), and harvesting followed by site preparation (Duchesne *et al.* 1999; Klimaszewski *et al.* 2005*a*), for making comparisons between silvicultural treatments and natural disturbances such as wildfire (Wikars 1995; Gandhi *et al.* 2001; Niwa and Peck 2002; Baker *et al.* 2004), and for determining effects of intensive fiber production, such as plantation forestry and ligniculture (Atlegrim *et al.* 1997; Allegro and Sciaky 2003; Finch 2005). In North America the extensive use of carabid beetles relative to other arthropod taxa has largely flowed from the relative accessibility of reliable taxonomy (Lindroth 1961, 1963, 1966, 1968, 1969*a*, 1969*b*), examples of the effective use of carabids as indicators of habitat change in Europe (Szyszko 1974, 1983; Thiele 1977), and the efforts of several key specialists who have encouraged carabidology (*e.g.*, Dr. George Ball at the University of Alberta), provided taxonomic support, or otherwise influenced many of the current researchers in the field. Another factor driving the widespread use of carabids as ecological indicators is that they are relatively well known biologically, with recent compilations of life-history and dietary information available for many species (Larochelle and Larivière 2003).

Although carabids have been used to assess stand-level effects of forest harvesting and natural disturbances such as wildfires, their effectiveness for evaluating larger scale changes in forest composition is less clear (Rykken *et al.* 1997). For agencies with large-scale regulatory or advisory mandates, such as federal and provincial government departments, the Canadian Council of Forest Ministers, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), and the Biological Survey of Canada, the efficacy of carabids as indicators of forest change at regional and larger scales has implications for the development of criteria and indicators used in developing approaches to sustainable forest management. A key question that has remained unanswered is whether consistent taxon-based indicators of forest change that can be applied across broad regional scales actually exist. Although most would agree that it is unlikely that any taxon-based indicator will be consistently related to the effects of the many forest-management strategies being implemented across forest ecosystems in Canada, understanding the practical limitations of specific taxonomic groups as indicators will further their implementation within monitoring programs.

In contrast to broad-scale indicators, species that respond to localized features (such as legacy elements and unique habitat features) will likely have important but different roles as biological indicators. A fundamental distinction between these two groups of indicators is the difference in frequency (occurrence) – abundance relationships (Kean and Bigelow 2004). Species that are relatively abundant, occur relatively frequently, and are consistently associated with given environmental conditions are by definition good ecological indicators (Dufrene and Legendre 1997). Species with this type of frequency–abundance relationship are promising candidates as indicators of the presence of "the given environmental conditions" at broad spatial scales. In general, these are the species effectively conserved by "coarse-filter" management, *i.e.*, the conservation of habitat features following forest management (Hunter 1991). Species not particularly well served by the standard coarse-filter approach fall into two groups. First, species that are locally abundant but geographically limited may reflect either important site-specific features or historical patterns. These species may be particularly important in identifying localized "hot spots" of diversity or areas of localized endemism (Patterson 1987) but are by definition limited in their application at broader spatial scales. These differences are arguably related to the difference between coarse-filter and fine-filter indicators proposed in ecosystem-based management. Second, a set of potentially useful indicators would include species that are both widespread and rare, and whose abundance reflects the existence of particular microhabitats necessary to conserve the fine-scale structure of forest environments. However, without an excellent understanding of their habitat requirements, such species are impractical to use as indicators because of limitations associated with sampling and detecting them. Nonetheless, these are the species most at risk under a coarse-filter approach, which may homogenize the fine-grain aspects of forest habitats (Spence and Volney 1999).

Comparisons of frequency–abundance relationships among species have also been increasingly used to evaluate patterns of biodiversity at large scales. Often these approaches rely on assumptions about a species' ability to disperse between habitat patches. In the special case of neutral approaches, frequency–abundance patterns are evaluated assuming that species have equal demographic potential and equal dispersal ability (Hubbell 2001; Volkov *et al*. 2003). Unfortunately, direct evaluations of carabid dispersal ability have been largely limited to nonforested ecosystems (Mascanzoni and Wallin 1986; Wallin and Ekbom 1988, 1994) as have large-scale mark–recapture efforts, such as the exemplary study by Boer (1981). In an alternative approach, several authors have attempted to link bionomic characteristics such as body size and wing morphology with dispersal ability (Niemela and Spence 1994; Gutierrez and Menendez 1997; Kotze *et al*. 2003; Kotze and O'Hara 2003; Ulrich and Zalewski 2006). Consideration of data about usual dispersal ability may likewise facilitate understanding of the potential of carabids as indicator species. For example, species with limited dispersal ability may be extremely sensitive indicators of changes in localized forest conditions. Species with a greater capacity for dispersal may be more appropriate for evaluating larger scale consequences of forest change.

Here we evaluate the efficacy of carabids as bioindicators of forest disturbance at local and regional scales using data from 10 large-scale forestry experiments across Canada. Our evaluation is based on comparing patterns of frequency of occurrence and abundance of species that are often attributed to the relative importance of regional or local factors (Hanski 1982; Gaston 1996; McGeoch and Gaston 2002). Typically, abundance–frequency distributions are characterized by a continuum of species that range from numerically abundant and geographically widespread to rarer, more localized species (Gaston 1996). Identifying widespread and localized indicators that respond consistently to forest change would be beneficial for developing useful coarse- and fine-filter strategies for maintaining biodiversity. Useful broad-scale indicators will be defined primarily by effects of forest management across broad cover-type and geographic differences. More localized indicators will respond to effects of forest management but will be nested in the environmental context of forest stand type and geographic region. We also compare bionomic characteristics, particularly those related to dispersal ability and habitat associations, of a relatively large number of carabid species in relation to frequency–abundance relationships. By comparing species traits we revisit the broader explanations for frequency–abundance relationships in carabids (Niemela and Spence 1994; Kotze *et al.* 2003; Kotze and O'Hara 2003; Ulrich and Zalewski 2006) but extend the discussion to the use of carabids as indicators of both anthropogenic and natural disturbances in Canadian boreal forests.

Materials and methods

Study sites

Information on carabid assemblages used in this analysis was compiled from 10 separate stand-level forestry studies across Canada (Table 1, Fig. 1). Each study used replicated experimental designs with experimental units ranging from several to hundreds of hectares. All studies evaluated the response of carabids to various management activities and natural disturbances, including clear-cut harvesting, partial cutting, gap cutting, soil preparations, prescribed and natural wildfire, postfire salvage logging, and recovery following insect outbreaks (Table 1). We included information from additional surveys of aspen stands from six areas located throughout Alberta. These 10 studies provided 365 experimental sites for our analysis. Location, silvicultural treatments, and dominant cover type, along with relevant citations for these experiments, are summarized in Table 1 and Figure 1. In all experiments carabids were collected using pitfall traps (Spence and Niemelä 1994; Digweed *et al*. 1995; Work *et al*. 2002). All material was identified to species.

Statistical analyses

We used sum-of-squares-based multivariate regression trees (ssMRT; De'ath 2002) to partition variance explained by geographic region, forest cover type, and forest harvesting, based on the MVPART algorithm available for the statistical computing language R. In contrast to indirect ordination methods such as nonmetric multidimensional scaling, the ssMRT is a direct classification method that successively subdivides the original data into smaller "nodes" that can be attributed to changes in environmental factors. This method does not rely on assumptions of linearity or Gaussian relationships with environmental gradients, unlike other direct classification methods such as canonical correspondence analysis (McCune and Grace 2002). Species responses were summarized at the stand level for each of these experiments. As sampling intensity varied among studies, data

Table 1. Experimental studies and surveys of the effect of silvicultural practices or natural disturbances on carabid beetle biodiversity used in multivariate analysis.

Study name	Location	Dominant forest cover type(s)	Sylvicultural treatment(s)/natural disturbance(s)	Date treatment applied	Sampling date	No. of experimental units used in analysis	Reference
Acadia Forest	New Brunswick	Red spruce	Clear-cutting, strip-cutting	1998–1999	1999–2000	9	Klimaszewski *et al.* 2005*b*
Aspen Studies	Across northern Alberta	Trembling aspen and balsam poplar	Successional comparison of aspen-dominated stands	1992–1993		32	
EMEND*	Northwestern Alberta	Boreal mixedwood	Variable retention Harvesting	1998–1999	1999–2000	100	Work *et al.* 2003
Parc des Grand-Jardins	Charlevoix, Quebec	Black spruce	Wildfire	Chronosequence (20, 50, and 80 years after fire)		20	
Hemlock Looper Recovery	Île d'Anticosti, Quebec	Balsam fir	Hemlock looper outbreak	25 years after outbreak		6	
Hinton	Foothills of Rocky Mountains, Alberta	Spruce and lodgepole pine	Clear-cutting	Chronosequence (1–27 years after clear-cutting)	1989–1991	20	Niemela *et al.* 1993
House River	Eastern Alberta	Boreal mixedwood	Salvage logging	2003–2004	2004	96	
SAFE[†]	Northwestern Quebec	Boreal mixedwood	Partial cutting, prescribed burning	1999	2004	15	Brais *et al.* 2004
SSAM	Northeastern Quebec	Yellow birch, balsam fir, and red spruce	Gap cutting and soil scarification	1999	2000	20 (36)	Klimaszewski *et al.* 2005*a*
Spruce budworm outbreak	Bas St-Laurent, Quebec	Balsam fir	Spruce budworm outbreak/salvage	20 years after outbreak		15	
Zama	Northern Alberta	White spruce	Partial cutting, feather cutting	1997–1998	1997–1999	16	

Note: The stands used at the Systèmes sylvicoles adaptés à la forêt mélangée (SSAM) project were further divided for gap and soil treatments. For our analysis we used the total number of treatment units, 36, that were used at SSAM.

*Ecosystem management emulating natural disturbance.

[†] Sylviculture et aménagement forestiers écosystémique.

Fig. 1. Locations of 10 large-scale experimental studies/surveys to measure changes in carabid assemblages in response to disturbances including forest harvesting, subsequent soil preparation, natural and prescribed wildfire, and insect outbreaks (EMEND, ecosystem management emulating natural disturbance; SAFE, Sylviculture et aménagement forestiers écosystémique; SSAM, Systèmes sylvicoles adaptés à la forêt mélangée).

were standardized by site totals and analyzed as relative abundances rather than absolute totals or cumulative catch rates. As a consequence, representations of relative abundance, such as species-abundance distributions, reflect the relative proportion of each species bounded by the upper limit of the number of sites, in this case 365. A total of 152 carabid species were considered in this analysis.

Differences in carabid composition were evaluated in terms of geographic location (Canadian province), silvicultural treatment, and dominant cover type. Silvicultural variables were summarized as 12 separate categorical variables. These treatments included 10 major treatments including uncut, partial cut, clear-cut, gap cut, strip cut, feather cut, selectively cut, salvage cut, prescribed burning, and one black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.; Pinaceae) plantation. Two additional treatments included light topsoil site preparation (soil scarification) following clear-cutting and gap cutting. Two sites were also used to evaluate the recovery of carabid communities following outbreaks of eastern spruce budworm (*Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae)) in the Bas St-Laurent region of Quebec, and eastern hemlock looper (*Lambdina fiscellaria fiscellaria* (Guenée) (Lepidoptera: Geometridae)) on the Île d'Anticosti in the Gulf of St. Lawrence. Stand cover type was summarized as deciduous, mixed, or coniferous, based on the dominant canopy cover. The size of the ssMRT or the number of nodes was chosen on the basis of cross-validation of 1000 randomizations of the original data set. We used indicator-species analysis (Dufrene and Legendre 1997) to evaluate individual species responses to splits defined by the ssMRT. All indicator analyses were done using the duleg algorithm from the LABDSV package available for the statistical computing language R. We report the status of species with indicator values greater than 40, as this value forms a natural upper break in the distribution of indicator values.

Bionomic information

Information on reproductive activity, dispersal ability, and habitat association was compiled for each species from Larochelle and Larivière (2003). Overall species phenology and periods of reproductive activity, including periods when gravid females or teneral adults were collected, were considered if recorded. Dispersal ability was measured in terms of wing morphology (macropterous, brachypterous, or wing polymorphic) and running ability (fast, medium, or slow), with additional information on climbing and burrowing being noted when available. Habitat associations were noted with particular reference to downed wood, rotten logs, and rotten stumps. These features may be used by some carabids as overwintering sites, resting places when not active, and oviposition sites. Body-size information (minimum and maximum body lengths) was compiled from Lindroth (1961, 1963, 1966, 1968, 1969*a*, 1969*b*). Additional data on geographic distribution of carabids in Canada were compiled from Bousquet and Larochelle (1993). Geographic range of a species was evaluated as the maximum number of provinces spanned by an east–west transect across Canada (exclusive of Yukon, Northwest Territories, and Nunavut). For this measure a score of 11 thus indicates a species with a trans-Canadian distribution and a score of 1 means that the species is restricted to a single province. We also included the total number of provinces to account for species with discontinuous distributions.

Results

Of the 152 species considered in this analysis, 16 species constituted 90% of the relative abundance (Table 2). Twelve of these dominant species have trans-Canadian distributions. Ninety-one less common species, or species that were collected from at least two experimental stands, composed 9.9% of the cumulative relative abundance. Of these species 42 had transcontinental distributions according to the criteria in Materials and methods. The remaining 45 species were collected from a single experimental site only, and composed less than 0.01% of the total relative abundance. One-third of these least abundant species were reported to have transcontinental or near-transcontinental distributions.

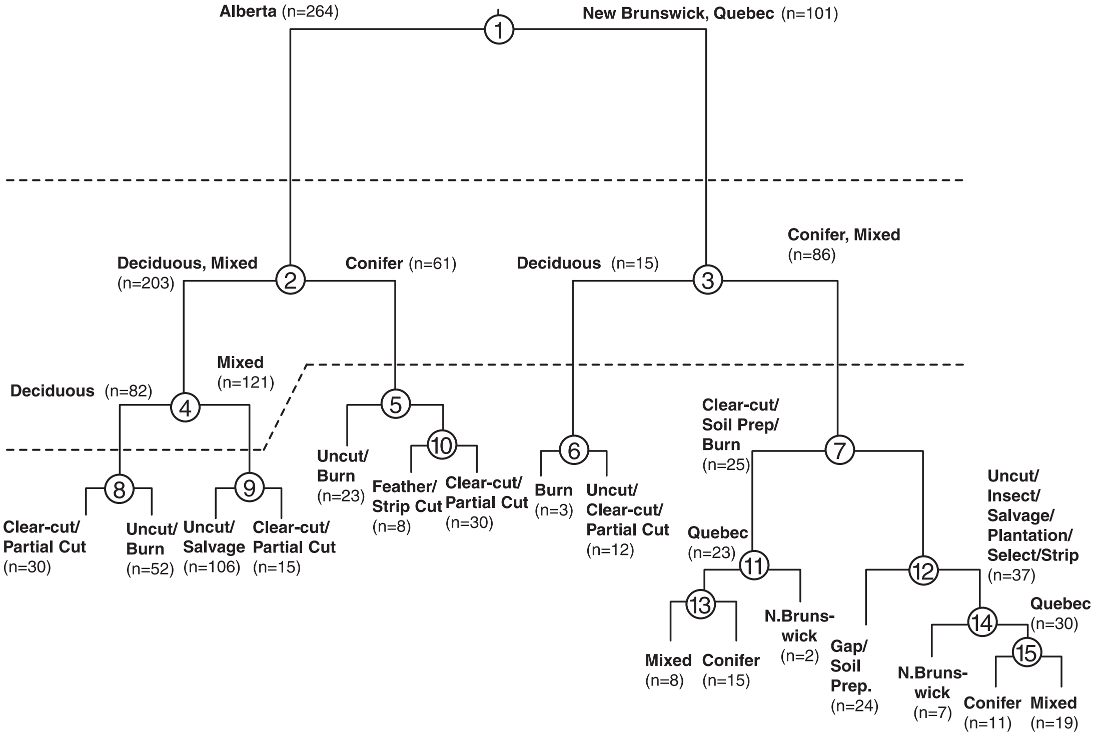
Cross-validations of the ssMRT produced a 16-node tree 991/1000 times (Fig. 2). This tree explained 47.5% of the total variance in carabid species composition, based on differences in geography, forest type, and disturbance type. The cross-validation error rate was 63.5% ± 0.32%. In general, basal splits of the tree highlighted hierarchical nesting of the three factors. Effects of silviculture and disturbance were nested within broader forest cover type that was in turn nested within broad geographic differences between eastern and western Canada in the basal portion of the tree. Limited recurrence of provincial and ecosystem differences was detected in the terminal portion of the multivariate regression tree. These additional splits occur in eastern coniferous and mixed stands following relatively complex "treatment" nodes that contained several silvicultural and disturbance factors. Within the hierarchical nesting described above, ecosystem differences accounted for 19.68% of the total variance, followed by the effects of silviculture and natural disturbance regime (14.12%) and variation among provinces (13.66%) (Table 3). When the total variance explained by the ssMRT was partitioned by individual species, 11 species accounted for 44.47% of the total variance. Each of these species accounted for at least 1% of the total variance explained (Table 3) and formed a subset of the dominant species shown in Table 2. The remaining 141 species accounted for 2.99% of the variance explained (Table 3). Thus, these sorts of large-scale patterns depended strongly on only about 7% of boreal carabid diversity in Canada.

The first split of the ssMRT partitioned carabid composition among stands located in eastern and western Canada (Fig. 3). Two species, *Pterostichus coracinus* (Newman) and *Synuchus impunctatus* (Say), were distinctly associated with eastern stands (Table 4). *Pterostichus coracinus* was absent from western stands, while *S. impunctatus* was less abundant in the west than in the east. Eight species were significantly associated with western stands (Table 4). Three species, *Agonum retractum* LeConte, *Calathus ingratus* Dejean, and *Platynus decentis* (Say), were associated primarily with western stands but were also found in relatively high numbers in eastern stands. In contrast, two dominant species, *Calathus advena* (LeConte) and *Stereocerus haematopus* (Dejean), and three less common species, *Carabus chamissonis* Fischer von Waldheim, *Calosoma frigidum* Kirby, and *Patrobus foveocollis* (Eschscholtz), were primarily associated with western stands and were much less abundant in eastern stands.

Table 2. Relative abundance, frequency, and distribution of 16 dominant carabid beetle species collected from 365 forest stands across Canada.

	Abundance		Frequency (occurrence)		Distribution	
	Relative abundance	Cumulative relative abundance	Frequency (total = 365)	Relative frequency	Geographic distribution score	No. of provinces
Pterostichus adstrictus Eschscholtz	0.23	0.23	346	0.95	11	11
Calathus ingratus Dejean	0.12	0.36	323	0.88	11	10
Stereocerus haematopus (Dejean)	0.09	0.45	233	0.64	11	8
Platynus decentis (Say)	0.09	0.53	299	0.82	11	11
Pterostichus pensylvanicus LeConte	0.05	0.59	221	0.61	11	10
Pterostichus coracinus Newman	0.05	0.64	78	0.21	7	7
Agonum retractum LeConte	0.06	0.70	268	0.73	11	10
Calathus advena LeConte	0.04	0.74	156	0.43	11	7
Carabus chamissonis Fischer	0.03	0.77	209	0.57	9	6
Sericoda quadripunctata (DeGeer)	0.03	0.80	93	0.25	11	10
Pterostichus punctatissimus Randall	0.02	0.82	168	0.46	11	10
Synuchus impunctatus Say	0.03	0.85	134	0.37	11	10
Calosoma frigidum Kirby	0.02	0.86	126	0.35	9	9
Scaphinotus marginatus Fischer	0.02	0.88	49	0.13	2	2
Patrobus foveocollis (Eschscholtz)	0.01	0.89	156	0.43	11	8
Trechus apicalis Motschulsky	0.01	0.90	141	0.39	11	10

Fig. 2. The sum of squares-based multivariate regression tree (ssMRT) used to classify 365 forest stands based on the response of 152 carabid species to nested effects of geography, cover type, and silvicultural and other disturbance-related factors. The ssMRT was selected 991/1000 cross-validated and explained 47.5% of the variance. The broken lines illustrate the initial hierarchical nesting of disturbance factors within forest cover types within geographical location. Variation explained by tree splits is further described in Table 3.



Within the subsequent eastern and western splits of the tree, cover-type differences were the next most important factor determining carabid composition. Within both regions, deciduous and coniferous stands differed in carabid composition, with mixed stands being initially grouped with one or the other of these stand types. Within the western split, deciduous and mixed stands were delineated from conifer-dominated stands based on the abundance of six species. Two dominant species, *P. decentis* and *A. retractum*, and two less common species, *C. frigidum* and *C. chamissonis*, were abundant in deciduous and mixed stands. *Stereocerus haematopus* and *C. advena* were most often found in coniferous stands (Fig. 4). Deciduous and mixed stands were subsequently divided in the ssMRT. *Agonum retractum, Pterostichus pensylvanicus* LeConte, and *P. decentis* were common species associated with deciduous stands. Less common species associated with deciduous stands were *C. frigidum* and *P. foveocollis*. In contrast, *S. haematopus* and *Sericoda quadripunctatum* (DeGeer) and the less commonly collected *C. chamissonis* were significantly associated with mixed stands (Fig. 4).

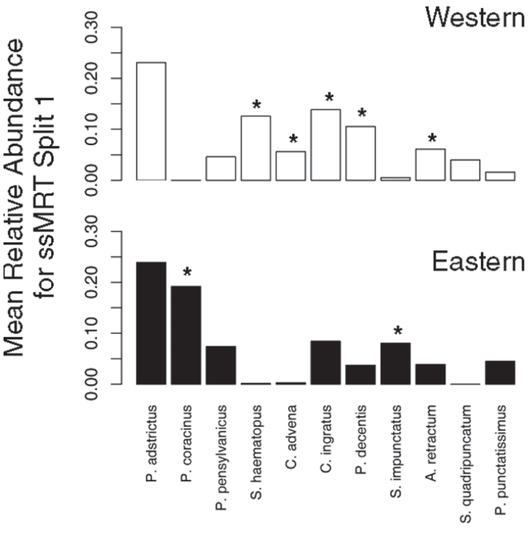
Deciduous stands within the eastern split were defined by *A. retractum, P. pensylvanicus,* and *S. impuncatus* as well as five less common species, *Harpalus uteanus* Casey, *Notiophilus aeneus* (Herbst), *Poecilus lucublandus* (Say), *Sphaeroderus lecontei lecontei* Dejean, and *Sphaeroderus canadensis canadensis* Chaudoir, while the mixed and conifer-dominated stands within that split were defined by *P. adstrictus* and *P. coracinus* (Fig. 5). Although mixed stands were initially grouped with coniferous stands, they were resolved as separate groups only in terminal nodes following complex interactions between disturbance and provincial differences. Interestingly, within the terminal nodes of the eastern split, no species were significantly associated with mixed or coniferous stands with an indicator value greater than 40.

Effects of disturbance regime appeared in subsequent divisions beyond initial geographic

Table 3. Variance explained by the 11 most dominant carabid beetle species and remaining less abundant species from the ssMRT.

	Tree split															
	1 Prov	2 Eco	4 Eco	8 Treat	9 Treat	5 Treat	10 Treat	3 Eco	6 Treat	7 Treat	11 Prov	13 Eco	12 Treat	14 Prov	15 Eco	Variance explained
Pterostichus adstrictus Eschscholtz	0.01	0.23	0.07	0.32	0.77	0.34	0.21	1.55	0.00	3.06	0.90	0.52	1.17	0.15	0.03	9.33
Pterostichus coracinus (Newman)	5.31	0.00	0.00	0.00	0.00	0.00	0.00	0.83	0.01	1.25	0.01	0.69	0.28	0.01	0.45	8.84
Pterostichus pensylvanicus LeConte	0.12	0.28	0.91	0.39	0.00	0.00	0.00	4.49	0.76	0.00	0.04	0.00	0.01	0.12	0.00	7.12
Stereocerus haematopus (Dejean)	2.22	2.16	0.64	0.06	0.06	0.03	0.74	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.91
Calathus advena (LeConte)	0.40	1.37	0.02	0.00	0.07	1.09	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	3.07
Calathus ingratus Dejean	0.42	0.02	0.00	0.02	0.01	0.12	0.02	0.17	0.00	0.43	0.00	0.00	0.77	0.37	0.01	2.36
Platynus decentis (Say)	0.66	0.74	0.10	0.24	0.05	0.01	0.01	0.00	0.00	0.07	0.00	0.00	0.01	0.01	0.03	1.93
Synuchus impunctatus (Say)	0.83	0.00	0.01	0.01	0.00	0.00	0.00	0.09	0.00	0.05	0.22	0.05	0.02	0.36	0.02	1.66
Agonum retractum LeConte	0.07	0.27	1.03	0.04	0.01	0.00	0.00	0.05	0.01	0.05	0.00	0.00	0.00	0.00	0.06	1.59
Sericoda quadripunctatum (DeGeer)	0.23	0.19	0.68	0.00	0.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.34
Pterostichus punctatissimus Randall	0.12	0.00	0.05	0.00	0.01	0.00	0.01	0.07	0.00	0.20	0.05	0.33	0.07	0.04	0.37	1.32
Variance explained by dominant species	10.39	5.26	3.51	1.08	1.22	1.59	1.1	7.25	0.78	5.11	1.22	1.59	2.33	1.06	0.98	44.47
Variance explained by remaining species	0.67	0.2	0.23	0.1	0.07	0.17	0.09	0.26	0.28	0.11	0.17	0.11	0.09	0.15	0.29	2.99
Total variance explained by each split	11.06	5.46	3.74	1.18	1.29	1.76	1.19	7.51	1.06	5.22	1.39	1.70	2.42	1.21	1.27	47.46

Fig. 3. Mean relative abundances of 11 carabid species associated with the initial split of the ssMRT attributable to geographic variation in carabid species composition among stands located in western and eastern Canada. An asterisk denotes a significant indicator value (>40).



and cover-type-derived splits. Within the western portion of the MRT, these terminal divisions consistently divided uncut stands and stands associated with fire events (such as prescribed burns or salvage logging following burns) from harvested stands (Fig. 2). We observed several species with a significant and relatively high indicator value associated with terminal nodes. *Carabus chamissonis*, *Pterostichus empetricola* (Dejean), *P. punctatissimus*, and *S. haematopus* were significantly associated with strip- and feather-cut stands in spruce-dominated ecosystems in western Canada. In the corresponding node of the ssMRT, *C. advena, P. foveocollis*, and *Bembidion grapii* Gyllenhal were associated with clear-cut and partial-cut sites. *Sericoda quadripunctata* was predominantly found in mixed stands that were either uncut or had been salvage-logged following wildfire. *Calathus advena* was also significantly associated with coniferous stands that were either burned or uncut (Table 4).

Despite the relatively few indicator species associated within western terminal nodes, major compositional differences between managed and unmanaged stands were predominantly linked with shifts in abundance of less common species, whereas the relative rank of dominant species was more stable (Fig. 6). For example, the relative rank of dominant taxa, specifically *P. adstrictus*, *C. ingratus*, and *S. haematopus,* differed little between managed and unmanaged stands. In contrast, differences in individual species responses between uncut/salvaged stands and harvested stands, as well as an increase in the variability of rank position, were more apparent among less common species than among dominant ones. The variability in rank position disappeared as a species became rare and was recorded only from a single location (Fig. 6).

The relative importance of geographic, ecosystem, and treatment differences was less clear beyond the initial ecosystem divisions in the eastern portion of the tree. Within the terminal nodes of eastern deciduous stands, a division between burned and unburned/harvested stands was defined by a preponderance of *Carabus meander* Fischer von Waldheim, *Hapalus egregeious* Casey, *Harpalus utaneaus* Casey, and *Poecilus lucublandis* (Say) (Table 4) as well as three less common species (*Acupalpus canadensis* Casey (indicator value (IV) = 21.5, p = 0.023), *Agonum affine* Kirby (IV = 21.7, p = 0.023), and *Chlaenius emarginatus* Say (IV = 24.5, p = 0.020)). Within unburned and harvested stands, *P. pensylvanicus*, *S. lecontei lecontei*, and *Trechus crassiscapus* Lindroth (Table 4), and to a lesser extent, *Clivina impressifrons* LeConte (IV = 16.6, p = 0.015) were significant indicators. Within eastern mixed and conifer stands, stands that experienced clearcutting, soil preparation, or prescribed burning were initially separated from a "catch-all" treatment node that contained stands that had experienced extensive insect outbreaks, salvage logging, selective logging, strip cutting, or were newly established as plantations. However, all effects of silviculture or disturbance treatment are ultimately confounded by geography and cover type. For example, 13 species were significant indicators of clearcut stands found only in New Brunswick (Table 4).

Relationship between bionomics and distribution

Although frequency of occurrence was strongly related to species abundance (relative frequency = 5.94 ± 0.292 × relative abundance + 13.53 ± 2.732 (mean ± SE), adjusted least square, r^2 = 0.73, P < 0.0001), bionomic information such as body size, wing morphology, and habitat associations showed little relationship with either abundance or frequency. Species characteristics often attributed to dispersal

Table 4. Significant indicator values (IV > 40) for carabid beetle species associated with four initial splits and

	MRT split 1			MRT split 2		
	Region	IV	*P*	Ecosystem*	IV	*P*
Agonum cupripenne (Say)						
Agonum retractum LeConte	West	48.6	0.003	Decid., Mix.	46.1	0.001
Agonum trigeminum Lindroth						
Batenus mannerhemi (Dejean)						
Bembidion grapii Gyllenhal						
Bembidion praticola Lindroth						
Bembidion properans Stephens						
Bembidion versicolor (LeConte)						
Calathus advena (LeConte)	West	54.5	0.001	Con.	65.1	0.001
Calathus ingratus Dejean	West	61.6	0.001			
Calosoma frigidum Kirby	West	46.3	0.001	Decid., Mix.	57.6	0.001
Carabus chamissonis Fischer	West	79.2	0.001	Decid., Mix	43.5	0.001
Carabus maeander Fischer						
Chlaenius sericeus (Forster)						
Harpalus egregious Casey						
Harpalus herbivagus Say						
Harpalus rubripes (Duftschmid)						
Harpalus rufipes (DeGeer)						
Harpalus uteanus Casey						
Notiophilus aeneus Herbst						
Notiophilus aquaticus (Linné)						
Patrobus foveocollis (Eschscholtz)	West	57.4	0.001			
Platynus decentis (Say)	West	67.6	0.001	Decid., Mix.	60.8	0.001
Poecilus lucublandus (Say)						
Pterostichus adstrictus Eschsholtz						
Pterostichus coracinus (Newman)	East	77.2	0.001			
Pterostichus empetricola Dejean						
Pterostichus pensylvanicus LeConte						
Pterostichus punctatissimus Randall						
Sericoda quadripunctata (DeGeer)						
Sphaeroderus canadensis canadensis Chaudoir						
Sphaeroderus lecontei lecontei Dejean						
Stenolophus conjunctus (Say)						
Stereocerus haematopus (Dejean)	West	86.7	0.001	Con	70.1	0.001
Synuchus impunctatus (Say)	East	65.3	0.001			
Syntomus americanus (Dejean)						
Trechus crassiscapus Lindroth						

*Con., coniferous; Decid., deciduous; Mix., mixed.

[†] N.B., New Brunswick.

[‡] *Bembidion praticola* was associated with uncut/insect/salvage/plantation/select/strip treatments.

terminal nodes derived from sum-of-squares-based multivariate regression tree (ssMRT) analysis.

MRT split 4			MRT split 3			MRT terminal splits			
Ecosystem*	IV	*P*	Ecosystem*	IV	*P*	Silviculture/ disturbance	Parental node[†]	IV	*P*
						Clear-cut	11 (N.B.)	82.7	0.001
Decid.	68.0	0.001	Decid.	44.6	0.01				
						Clear-cut	11 (N.B.)	50.0	0.001
						Clear-cut	11 (N.B.)	50.0	0.001
						Clear-cut / partial cut[‡]	10	42.2	0.001
							11 (N.B.)	73.3	0.001
						Clear-cut	11 (N.B.)	50.0	0.001
						Clear-cut	11 (N.B.)	85.3	0.001
						Burn, uncut	5	45.8	0.003
						Clear-cut / partial cut	10	56.4	0.002
Decid.	57.0	0.001							
Mix.	40.9	0.001				Feather and strip cut	10	66.1	0.001
						Burn	6	62.2	0.001
						Clear-cut	11 (N.B.)	66.9	0.001
						Burn	6	99.1	0.001
						Clear-cut	11 (N.B.)	50.0	0.001
						Clear-cut	11 (N.B.)	50.0	0.001
						Clear-cut	11 (N.B.)	57.3	0.002
			Decid	93.3	0.001	Burn	6	73.6	0.002
			Decid.	43.5	0.001				
						Clear-cut	11 (N.B.)	45.9	0.003
Decid.	47.5	0.001				Clear-cut / partial cut	10	41.9	0.003
Decid.	49.0	0.001							
			Decid.	45.8	0.001	Burn	6	84.0	0.001
			Mix., Con.	43.8	0.003				
			Mix., Con.	64.5	0.001				
						Feather and strip cut	10	49.4	0.001
Decid.	61.9	0.001	Decid.	88.3	0.001	Clear-cut, partial cut, uncut	6	47.3	0.001
						Feather and strip cut	10	48.5	0.032
Mix.	68.8	0.001				Salvage, uncut	9	69.6	0.001
			Decid.	44.4	0.001				
Mix.	43.9	0.001	Decid.	97.4	0.001	Clear-cut, partial cut, uncut	6	47.3	0.001
						Clear-cut	11 (N.B.)	50.0	0.001
						Feather and strip cut	10	61.0	0.001
			Decid.	63.4	0.001				
						Clear-cut	11 (N.B.)	50.1	0.003
						Clear-cut, partial cut, uncut	6	40.2	0.001

Fig. 4. Mean relative abundances of 11 carabid species associated with the "western" split of the ssMRT attributable to differences in carabid species composition between deciduous/mixed stands and conifer-dominated stands and the subsequent division of deciduous and mixed stands. An asterisk denotes a significant indicator value (>40).

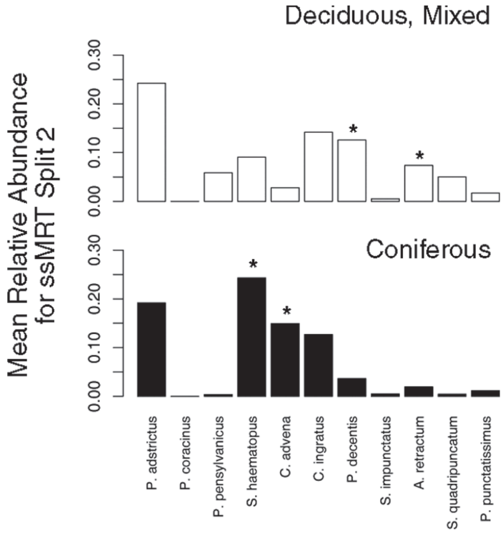
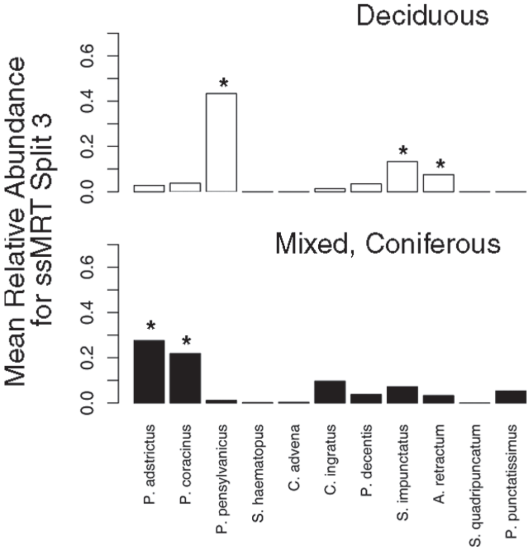
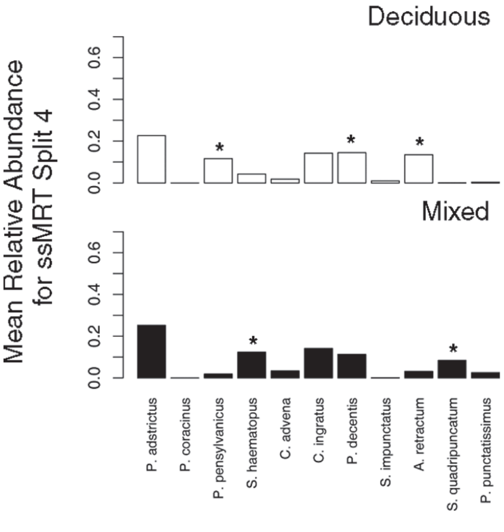


Fig. 5. Mean relative abundances of 11 carabid species associated with the "eastern" split of the ssMRT attributable to differences in carabid species composition between mixed/coniferous stands and deciduous-tree-dominated stands. An asterisk denotes a significant indicator value (>40).





capacity, such as increased body size (Fig. 7) or the presence of fully developed wings (Fig. 8), were not associated with abundant, widely distributed species, nor were they conspicuously absent in the group of rare taxa. Similarly, the occurrences of species with an affinity for downed wood reported in Larochelle and Larivière (2003) were not related to the relative abundance or occurrence of the species (Figs. 9, 10) (*i.e.*, species reported to have a strong affinity for downed wood were represented by both dominant and rare species).

Discussion

Despite the relatively large proportion of species with trans-Canadian distributions, regional and ecosystem differences in carabid composition limit the applicability of individual carabid species as indicators at a uniform national scale. This is evidenced by the initial MRT splits that attributed nearly twice as much of the total variation to regional and cover-type differences as to silvicultural or other disturbance factors. Thus, regional and cover-type differences provide a significant ecological context for the effects of silviculture and disturbance on the composition of forest carabid assemblages. This context-dependence must be considered in developing large-scale monitoring strategies and in discussions of criteria and indicators relevant to conservation. Regional differences in carabid fauna were attributed in part to shifts in dominance of species with a trans-Canadian distribution. Careful, biologically informed comparisons of variation in abundance of these species across regions, particularly among similar experimental studies, may give significant insight into larger scale mechanisms that regulate diversity and explain regional shifts in dominance.

The consistent finer scale differences in carabid composition among the three cover types also underscore the suitability of carabids as ecological indicators at the stand level. Differences in carabid composition between stands dominated by deciduous and coniferous species were indicated by strong affinities for either stand type, although again, species responses were often regionally restricted. Mixed stands may be particularly important from a faunal-management perspective, as they occupy an intermediate position between deciduous and coniferous stands in terms of carabid composition, as is seen in the ecosystem splits of the ssMRT. Dominant species with a strong affinity for deciduous or coniferous stands were often found in moderate abundance within mixed stands. For example, in the western region, abundances of *C. advena*, *P. adstrictus*, and *S. haematopus* peaked in coniferous stands, but these species were also found in mixed stands, although in more moderate abundance. Likewise, *P. decentis*, a dominant species in deciduous stands, was found in moderate abundances in mixed stands.

In proposed "multicohort" management strategies (Bergeron and Harvey 1997; Harvey *et al.* 2002) that aim at emulating natural disturbances, mixed stands significantly determine the overall forest structure. In forest succession, these stands are often viewed as transition elements that can be managed to promote old-growth characteristics by partial cutting, or to reinitiate succession, or to emulate the effects of stand-replacing disturbances, such as wildfire, through clear-cutting. Our results suggest that mixed stands may also represent transitional elements for biodiversity. Moreover, the compositional similarity of carabid assemblages from deciduous and mixed to coniferous stands differs between eastern and western Canada. This is evident from the recurrent "ecosystem" nodes in the terminal branches of the eastern portion of the ssMRT. These recurrent nodes may be related to increased compositional diversity of tree species within mixed stands in the eastern study sites. In Canada, it may be necessary, therefore, to view carabid indicators with a finer scale lens in eastern stands than in western stands. Overall, more carabid species are likely to be retained on a greater proportion of the landscape through the development of forest-management strategies that embrace mixedwoods than through the attempts to divide the land base between coniferous and deciduous stands that have characterized recent silvicultural prescriptions in Alberta and elsewhere.

The responses of carabid assemblages to silvicultural and disturbance factors were remarkably consistent within the context of the three ecosystem types in western Canada. The carabid fauna associated with uncut or burned stands (or stands that had experienced salvage logging following the massive House River fire, which burned ~3000 km^2 of woodlands near Lac La Biche in northeastern Alberta in the spring of 2002) was consistently different from the fauna associated with harvesting. Although uncut and burned stands repeatedly differed from harvested stands, we did not observe consistent responses of carabid species in these stand groups, and the number of indicator species associated with terminal nodes of the ssMRT was limited. Such associations probably reflect the relative stability of dominant species between managed and unmanaged stands; for example, the relative ranks of the dominant species *P. adstrictus*, *C. ingratus*, and *S. haematopus* changed little between managed and unmanaged stands. We attribute the differences between managed and uncut/salvaged stands in the ssMRT to important differences in the less common and rare species. This observation underscores the importance of explicit targeting of rare species in biomonitoring programs (Martikainen and Kouki 2003).

The relatively high variability among less common species also illustrates site-to-site differences that are inherent in any comparison at that scale. This is consistent with the "satellite species" concept, described within the core-satellite hypothesis (Hanski 1982), and may be closely associated with important site-specific features such as coarse woody debris, nondominant tree species, or unique soil/climatic conditions, some of which (*e.g.*, coarse woody debris) can be easily employed as secondary coarse filters after cover type. Although determining site-specific features that drive local patterns of diversity is beyond the scope of this study, many of these are likely to be legacy elements from past disturbances and stand history. This area has only begun to be studied (D.W. Langor, unpublished data).

The variable response of rare taxa to site-specific conditions and the importance of ecosystem and regional factors in determining carabid

Fig. 6. Mean ranks of species associated with unmanaged and managed forest stands in western Canada. Open bars denote responses of species within unmanaged stands, with the black line indicating mean rank; solid bars denote species responses within managed stands, with the the shaded line indicating mean rank. Narrow boxplots denote relatively consistent species ranks within either unmanaged or managed stands; wide boxplots denote shifts in species rank within either group of stands. Differences between boxplots denote differential changes in species rank between unmanaged and managed stands. Rank positions of dominant species are relatively stable compared with those of less common species of intermediate rank. Species with unchanging ranks, single occurrences of species, or rare species are indicated only by central tendency marks of boxplots. Species ranks along the *x* axis are not plotted on a linear scale. Species are ordered according to decreasing cumulative abundance and exclude species associated with eastern stands.

composition suggest two important lessons for future and proposed monitoring schemes. First, monitoring programs must be extensive enough to resolve responses of "rarer" species. Otherwise, these programs will merely provide lists of ubiquitous species that likely show no particularly interesting or worrisome response to forest change. Second, monitoring schemes should be designed so as to adequately reflect the ecosystem and to embrace the within-stand variability characteristic of the target region. The effectiveness of strategies lacking an ecologically meaningful stratification of finer scale factors such as ecosystem differences will likely be limited.

It should be noted that most of the studies included here represent initial species responses measured within 5 years of a natural disturbance or harvest. Also, most of the data came from studies that were limited to 1–2 years in duration. Proper evaluation of long-term planning objectives in forest management will require long-term data or, at a minimum, chronosequence data on various successional stages of regenerating forests. Thus, our conclusions made here should be corroborated by further evaluations of forest "recovery" following disturbance over time frames relevant to forestry.

Our study corroborated the positive relationship between the abundance of a given species and its frequency of occurrence reported in other carabid studies (Niemelä and Spence 1994; Gutierrez and Menendez 1997; Kotze and O'Hara 2003; Kotze *et al*. 2003; Ulrich and Zalewski 2006). However, in contrast to prior studies, we did not observe a clear association between frequency–abundance relationships and body size and (or) dispersal ability. Both Gutierrez and Menendez (1997) and Kotze *et al*. (2003) found a positive relationship between body size and frequency–abundance, although this finding was restricted to brachypterous species in Gutierrez and Menendez (1997). We did not observe this relationship even when brachypterous species were treated separately. Ulrich and Zalewski (2006) observed that rare, infrequent species are characterized as good dispersers. The lack of relationship between body size or wing condition and the frequency–abundance of a species in our study can be interpreted in several ways. First, interpretations of dispersal ability based on body size or wing condition may be flawed. For most carabid species quantitative evidence of dispersal ability is lacking. Consequently, a direct evaluation of the relationship between morphological traits and dispersal capability is difficult. Furthermore, the flight ability of a carabid may reflect larval feeding history, and adults may be able to fly only in some years (Aukema 1995). As many researchers have assumed that wing condition influences dispersal, particularly of species with dimorphic populations (*e.g.*, *Pterostichus melanarius* Illiger), it is generally supposed that dispersal by flight results in greater net dispersion of populations than does cursorial movement, especially in forest-dwelling populations (see Weber 1996). Also, if morphological traits do indeed correlate well with dispersal ability, current frequency–abundance patterns may reflect the historic spread of populations rather than an inherent advantage in dispersal ability *per se*. Unfortunately, we cannot resolve these issues without extensive quantitative investigation of the dispersal ability of these species.

In the context of biological indicators, the general lack of understanding about factors affecting dispersal should serve as a cautionary note to conservation biologists and landscape planners alike. Coarse-filter management has become the major mitigating strategy used to maintain biodiversity in managed forest landscapes (Larsson and Danell 2001; Work *et al*. 2003). Along with this perspective, many of the principles of landscape ecology, particularly the role of dispersal, have been readily adopted as a

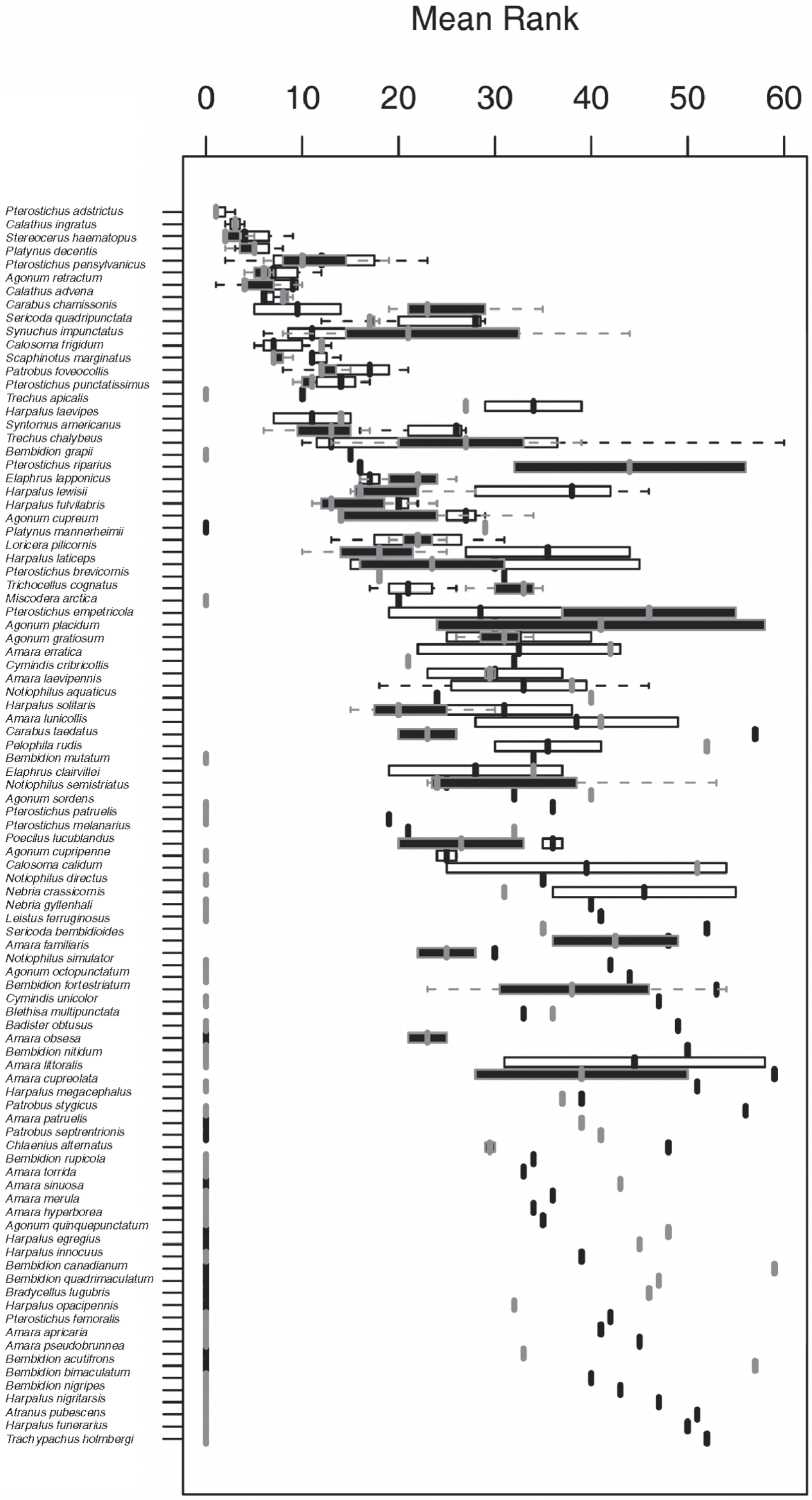

Mean Rank
0
10
20
30
40
50
60
Pterostichus adstrictus
Calathus ingratus
Stereocerus haematopus
Platynus decentis
Pterostichus pensylvanicus
Agonum retractum
Calathus advena
Carabus chamissonis
Sericoda quadripunctata
Synuchus impunctatus
Calosoma frigidum
Scaphinotus marginatus
Patrobus foveocollis
Pterostichus punctatissimus
Trechus apicalis
Harpalus laevipes
Syntomus americanus
Trechus chalybeus
Bembidion grapii
Pterostichus riparius
Elaphrus lapponicus
Harpalus lewisii
Harpalus fulvilabris
Agonum cupreum
Platynus mannerheimii
Loricera pilicornis
Harpalus laticeps
Pterostichus brevicornis
Trichocellus cognatus
Miscodera arctica
Pterostichus empetricola
Agonum placidum
Agonum gratiosum
Amara erratica
Cymindis cribricollis
Amara laevipennis
Notiophilus aquaticus
Harpalus solitaris
Amara lunicollis
Carabus taedatus
Pelophila rudis
Bembidion mutatum
Elaphrus clairvillei
Notiophilus semistriatus
Agonum sordens
Pterostichus patruelis
Pterostichus melanarius
Poecilus lucublandus
Agonum cupripenne
Calosoma calidum
Notiophilus directus
Nebria crassicornis
Nebria gyllenhali
Leistus ferruginosus
Sericoda bembidioides
Amara familiaris
Notiophilus simulator
Agonum octopunctatum
Bembidion fortestriatum
Cymindis unicolor
Blethisa multipunctata
Badister obtusus
Amara obsesa
Bembidion nitidum
Amara littoralis
Amara cupreolata
Harpalus megacephalus
Patrobus stygicus
Amara patruelis
Patrobus septentrionis
Chlaenius alternatus
Bembidion rupicola
Amara torrida
Amara sinuosa
Amara merula
Amara hyperborea
Agonum quinquepunctatum
Harpalus egregius
Harpalus innocuus
Bembidion canadianum
Bembidion quadrimaculatum
Bradycellus lugubris
Harpalus opacipennis
Pterostichus femoralis
Amara apricaria
Amara pseudobrunnea
Bembidion acutifrons
Bembidion bimaculatum
Bembidion nigripes
Harpalus nigritarsis
Atranus pubescens
Harpalus funerarius
Trachypachus holmbergi

Fig. 7. Comparison of carabid body sizes (circle size is proportionate to mean body length) with frequency – relative abundance relationships for 152 species collected from 365 forest stands located across Canada. To conserve space, expressions on the axes have been abbreviated from 1×10^{-3} to 10^{-3}, *etc*.

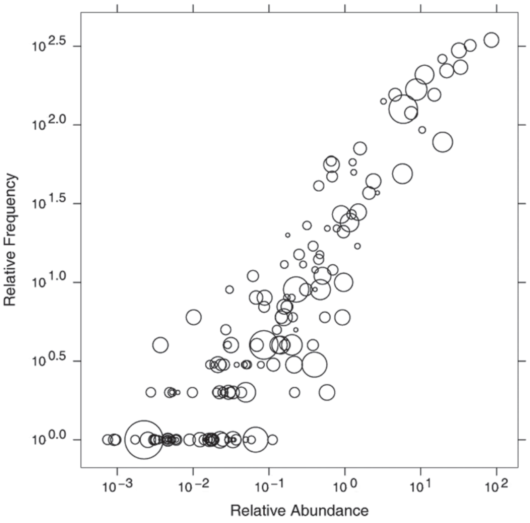


Fig. 8. Comparison of carabid wing morphology (macropterous (●), polymorphic (■), submacropterous (◇), brachypterous (○), no data available (+)) with frequency – relative abundance relationships for 152 species collected from 365 forest stands located across Canada. To conserve space, expressions on the axes have been abbreviated from 1×10^{-3} to 10^{-3}, *etc*.

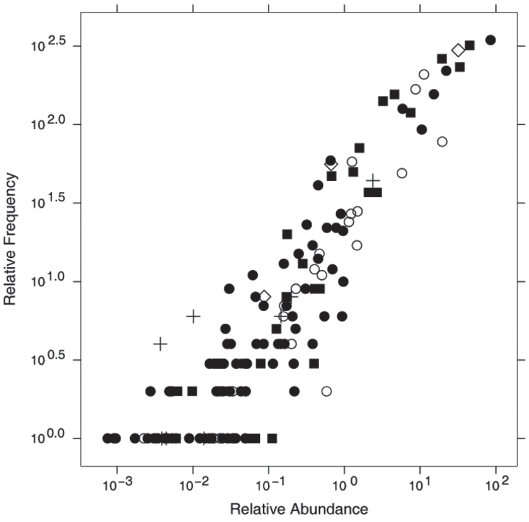


Fig. 9. Comparison of reported associations with logs (positive association (+), no specific relationship reported (○)) with frequency – relative abundance relationships for 152 species collected from 365 forest stands located across Canada. To conserve space, expressions on the axes have been abbreviated from 1×10^{-3} to 10^{-3}, *etc*.

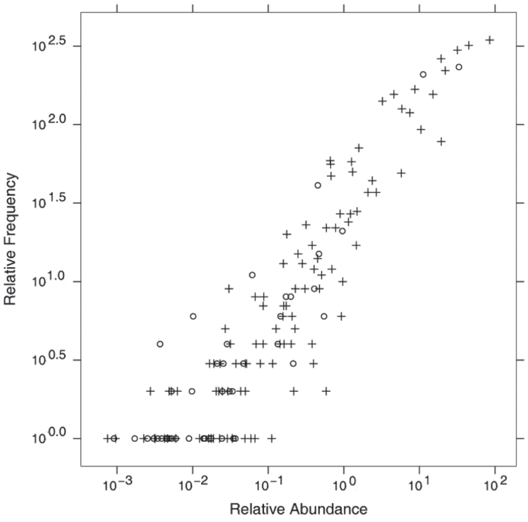
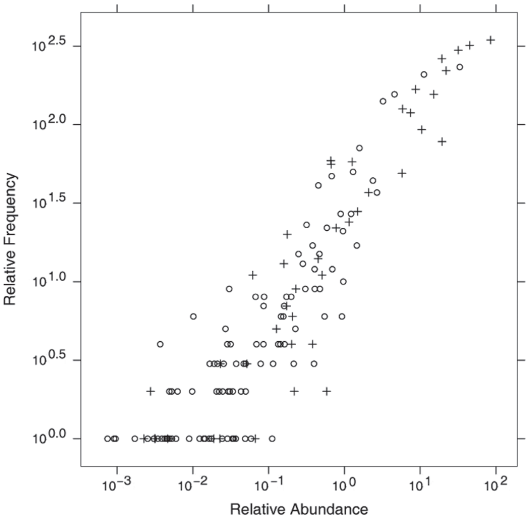


Fig. 10. Comparison of reported associations with dead wood beyond reported associations with logs with frequency – relative abundance relationships for 152 species collected from 365 forest stands located across Canada. These descriptions included more detailed associations such as "found under bark", "within rotting stumps", *etc*. (positive association (+), no specific relationship reported (○)). To conserve space, expressions on the axes have been abbreviated from 1×10^{-3} to 10^{-3}, *etc*.



justification for coarse-filter conservation. Although dispersal certainly plays an important role in maintaining some taxa (such as birds and mammals) at the scale of forest operations, we have little empirical evidence to either support or discount the role of dispersal in maintaining carabid populations. And although appealing in the context of landscape ecology, it may be neither prudent nor parsimonious to adopt unsubstantiated estimates of dispersal in lieu of other explanations such as the availability of habitats or resources within stands. These factors may well explain species abundance without invoking additional assumptions regarding dispersal ability.

Carabids have been largely excluded from discussions about the importance of within-stand features such as coarse woody debris, even though some species are found to depend critically on this resource (Goulet 1974). Our comparison of habitat affinities and frequency–abundance relationships suggests that a relatively large number of species use downed wood in some capacity, either as diurnal shelter or for more complex interactions such as oviposition or foraging. Association with downed wood was prevalent among both rare and dominant species. The relatively large number of species associated with decaying wood, together with the relative ubiquity of this association across dominant and rare species, suggests that carabids should be considered in discussions of downed-wood management.

The development of this new approach to evaluating carabid beetles as biodindicators has highlighted several areas of research that warrant further attention. These areas fall into the often undervalued category of natural history. Thanks to the extensive use of pitfall traps in ecological studies, we have developed a relatively good understanding of general habitat associations and distributions of a large number of species. However, this is based almost solely on interpretation of the distribution patterns of adult beetles. We lack the information that may be critical to evaluations of habitat preference and habitat quality, namely the distribution of larvae (see Spence 1979). This situation persists in part because of the lack of adequate taxonomic keys for larvae analogous to the work of Lindroth on adult carabids in North America (but for central and northern Europe see Luff 1993). Detailed information about habitat associations of larvae may provide a clearer view of the kinds of structure that should be maintained in managed forests. Because of the relatively limited mobility of larvae in comparison with adults, habitat associations of carabid larvae could be used to further refine our view of coarse-filter management and thus improve the overall efficiency of these conservation strategies.

Acknowledgements

We thank the numerous field assistants involved in the data collection, specimen sorting, and identification phases of each of these projects. Funding for individual studies was provided by various provincial and federal sources. Industrial support for the portion of the EMEND project presented here was provided in part by Canadian Forest Products and Daishowa–Marubeni and the Manning Diversified Trust Fund.

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