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Catastrophic windstorm and fuel-reduction treatments alter ground beetle (Coleoptera: Carabidae) assemblages in a North American sub-boreal forest

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ABSTRACT

We studied the short-term effects of a catastrophic windstorm and subsequent salvage-logging and prescribed-burning fuel-reduction treatments on ground beetle (Coleoptera: Carabidae) assemblages in a sub-boreal forest in northeastern Minnesota, USA. During 2000–2003, 29,873 ground beetles represented by 71 species were caught in unbaited and baited pitfall traps in aspen/birch/conifer (ABC) and jack pine (JP) cover types. At the family level, both land-area treatment and cover type had significant effects on ground beetle trap catches, but there were no effects of pinenes and ethanol as baits. Six times more beetles were trapped in the burned forests than in the other land-area treatments; more beetles were caught in undisturbed than in wind-disturbed sites, and one-third more beetles were caught in the ABC than in the JP cover type. Thus, the windstorm generally reduced the activity-abundance of the beetles, but prescribed-burning increased it. Both salvaged and burned forest plots (especially in the ABC cover type) had the greatest species richness, diversity, and the most unique species assemblages. There was a highly similar ground beetle species composition (nearly 100%) between the ABC and JP burned forests, indicating that burning was a more primary driver of composition than cover type. At the species level, *Pterostichus melanarius*, an invasive ground beetle from Europe and a cover type generalist, was the most abundant beetle in the study (one-third of the total catch), and was caught in greatest numbers in burned forests. Removal of *P. melanarius* from the species composition analyses altered similarities among cover types and land-area treatments. *Sphaeroderus nitidicollis brevoorti* and *Myas cyanescens* were caught exclusively in the ABC and JP cover type, respectively; two rare pyrophilous species, *Sericoda obsoleta* and *Sericoda quadripunctata*, were only caught in burned sites; three forest species, *Pterostichus coracinus*, *P. pensylvanicus*, and *Sphaeroderus lecontei*, were caught more often in undisturbed JP sites; and two frequently trapped, open-habitat species, *Agonum cupripenne* and *Poecilus l. lucublandus*, were nearly absent from the undisturbed and wind-disturbed sites, as salvage-logging had a significant positive effect on their activity-abundance. Most species of *Amara* and *Harpalus* were trapped only in the salvaged or burned sites, indicating invasion of these disturbed sites by open-habitat species. We conclude that both the combined effect of fuel-reduction activities subsequent to the wind event and the numerical response of the invasive *P. melanarius* to habitat disturbances can alter the short-term succession of ground beetle assemblages in the sub-boreal forest.

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1. Introduction

Small- and large-scale windstorms and wildfire are among the primary causes of tree-fall and forest disturbance in sub-boreal temperate forests (Heinselman, 1973; Bormann and Likens, 1979; Dunn et al., 1983; Canham and Loucks, 1984; Perry, 1994; Katovich et al., 1998; McCarthy, 2001). Wind-disturbances frequently determine tree species composition and age structure in these forests (Frelich and Reich, 1995; Palik and Robl, 1999; Arévalo

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et al., 2000), and yet, the responses of fauna that inhabit these disturbed forests are not well studied (Bouget and Duelli, 2004; Gandhi et al., 2007). One of the recent approaches to sustainable forestry has been to retain the integrity of forested ecosystems through emulation of natural disturbances *via* timber harvesting patterns (Thompson and Welsh, 1993; Angelstam, 1997; Gilmore, 1997). For this reason, it is imperative to study the effects of all interacting natural disturbances (e.g., windstorms, ice storms, wildfires, flooding, drought, and insect and disease outbreaks) on faunal assemblages.

On the 4th of July 1999, an unprecedented storm with wind derechos (straight-line winds with multiple downbursts) of over 145 km h^{-1} traveled over 3219 km, beginning in North Dakota; moving through Minnesota, Ontario, and Quebec; and ending in New England [National Oceanic and Atmospheric Administration (NOAA), 2006]. This international progressive windstorm, known as the "Boundary Waters-Canadian Derecho," lasted for over 22 h, and was one of the northernmost derechos recorded for North America (NOAA, 2006). In the Superior National Forest of northeastern Minnesota, this storm resulted in windthrow of over 193,000 ha of forestland with over 85% tree-fall in the unmanaged Boundary Waters Canoe Area Wilderness (BWCAW), and the managed Gunflint Trail Corridor (USDA Forest Service, 2000). This catastrophic windstorm provided us with a unique opportunity to study short-term faunal successional pathways following a large-scale and long-interval (>1000 years) disturbance. In Minnesota, most of the windthrow occurred on two major forest cover types: aspen/birch/conifer (ABC) and jack pine (JP). With dead and downed trees (fuel loads) exceeding 16,000 kg/ha in some of the wind-disturbed areas (Gilmore et al., 2003), there was a strong potential for the occurrence of other natural disturbances such as wildfire, or insect and disease outbreaks. In response to this threat, the USDA Forest Service reduced the fuel load along the Gunflint Corridor through two fuel-reduction treatments: (a) salvage-logging (1100 ha), and (b) prescribed-burning (860 ha). Despite these efforts, major wildfires occurred in and around the BWCAW in 2006 and 2007 (USDA Forest Service, 2007).

There is an absence of information regarding the impact of wind-disturbances and/or fuel-reduction treatments on the responses of the local insect fauna in the sub-boreal forest that characterizes the northern Great Lakes region of North America. In boreal forests, a large number of specialist insect species are hypothesized to be adapted to periodic natural disturbances (Holliday, 1984,1991; Danks and Foottit, 1989; Muona and Rutanen, 1994; Spence et al., 1997; Gandhi et al., 2001). In other systems, it is further hypothesized that these specialist species are sensitive to additional structural changes in the landscape resulting from post-wind-disturbance silvicultural treatments (Lindenmayer et al., 2004). Several workers have investigated the influence of salvage-logging after a wildfire on plant and animal taxa in Australian (Lindenmayer et al., 1999), Indonesian (Nieuwstadt et al., 2001), and Canadian (Morissette et al., 2002) forests. In addition, several studies have examined the influence of salvage-logging following a wind-disturbance event on insects in European (Duelli et al., 2002; Wermelinger et al., 2002) and on vegetation in Appalachian forests (Elliot et al., 2002). Similar research needs to be conducted in sub-boreal forests to assess the responses of insects to the combination of these land-area treatments after a severe wind-disturbance event.

Among terrestrial insects, ground beetles (Coleoptera: Carabidae), as predators (and rarely as herbivores) are important in forest litter decomposition and nutrient cycling, and overall maintenance of soil structure in forest ecosystems (Spence et al., 1997). These communities of beetles are sensitive to changes in environmental quality and habitat. Furthermore, as a 'non-target' taxon in most forest management plans, ground beetles are excellent indicators of forest changes because they are species-rich, numerically abundant, taxonomically stable, and can be caught by standardized trapping methods (McGeoch, 1998). Regional studies have revealed that Minnesota and surrounding states and provinces harbor diverse ground beetle assemblages that can be used as indicators of forest disturbances (Epstein and Kulman, 1990; Werner and Raffa, 2000, 2003; MacLean, 2002; Gandhi et al., 2005; Latty et al., 2006). In this study, conducted in the sub-boreal forest of northeastern Minnesota, our objectives were: (1) to determine if there were differences in ground beetle trap catches, species richness, diversity, and composition among the undisturbed, wind-disturbed, and subsequently managed (wind-disturbed-salvage-logged, and wind-disturbed-prescribed-burned) forest sites; and (2) to determine if there were differences in the same attributes between the ABC and JP forest cover types.

2. Materials and methods

2.1. Study plots

Ground beetles were sampled from the 32 study plots located in the BWCAW and along the Gunflint Trail Corridor in the Superior National Forest in Cook County, Minnesota, USA (Table 1) (Gandhi et al., 2005). Mean annual temperature of the region is 1–2 °C (Baker and Strub, 1965), and mean annual precipitation is 65–75 cm (Baker and Kuehnast, 1978). This area is located in the Laurentian mixed forest ecological province, northern Superior uplands section, and border lakes subsection of Minnesota (Minnesota Department of Natural Resources, 1999). The aspen/birch/conifer, *Populus tremuloides* Michx./*Betula papyrifera* Marsh./conifer (ABC) sites are on deeper, moist, well-drained till, outwash and lacustrine deposits, and loamy Entisols soil type [Land Type Associations (LTA) 14, 22, 23, 37]. The jack pine, *Pinus banksiana* Lamb. (JP) sites are on shallow, well-drained till and outwash deposits, and sandy Inceptisols soil type (LTA 21, 23) (USDA Forest Service, 2000; Anderson et al., 2001). The JP forests had originated after a wildfire, whereas the ABC forests had originated after clear-cutting (M. Theimer, USDA Forest Service, Superior National Forest, personal communication). Soil pH, mean age, and overall basal area were similar in both cover types, but basal areas by species varied between the two cover types (Table 2). These overstory attributes were recorded from sample plots between 1999 and 2002. The understory (shrub and forb) layers for these two cover types were assessed on co-located vegetative sampling plots (Supplementary data, Gilmore et al., 2005). Beaked-hazel, *Corylus cornuta* Marsh., and mountain maple, *Acer spicatum* Lamarck, were the dominant tall shrubs within the ABC cover type, whereas red raspberry, *Rubus idaeus* L., thimbleberry, *Rubus parviflorus* Nuttall, and bush-honesuckle, *Diervilla lonicera* Miller, tended to dominate the low shrubs. In the JP cover type, the low shrub bush-honeysuckle and the forb low-sweet blueberry, *Vaccinium angustifolium* Aiton, were dominant.

2.2. Experimental design

Ground beetles were sampled during the summers of 2000–2003 in the ABC and JP cover types. The plots were 2–3 ha in size, and were located at least 500 m away from each other to ensure independent samples. Four plots (replicates) in each of the two cover types were established in each of four land-area treatments as follows: (1) undisturbed; (2) severely wind-disturbed (>70% tree mortality); (3) wind-disturbed-salvage-logged (salvaged); and (4) wind-disturbed-prescribed-burned (burned) forests (Table 1). The prescribed-burned plots were also salvage-logged

Table 1
Geographical locations and names of 32 aspen/birch/conifer and jack pine study plots in the Superior National Forest, Cook Co., Minnesota, USA

Cover type	Land-area treatment	Plot name	Location
Aspen/Birch/Conifer	Undisturbed	Rudy[a]	48°2′42″N, 90°21′58″W
		East Bearskin	48°1′56″N, 90°23′55″W
		Flour Lake	48°1′56″N, 90°23′56″W
		North Poplar[a]	48°3′42″N, 90°33′55″W
	Wind-disturbed	Rudy[a]	48°2′35″N, 90°22′30″W
		East Bearskin	48°2′26″N, 90°23′37″W
		Flour Lake	48°2′42″N, 90°21′58″W
		North Poplar[a]	48°3′30″N, 90°32′40″W
	Salvaged	Rudy[a]	48°2′11″N, 90°23′1″W
		East Bearskin	48°1′46″N, 90°23′53″W
		Flour Lake	48°1′45″N, 90°24′18″W
		North Poplar[a]	48°3′42″N, 90°32′40″W
	Burned	Brule River	48°0′30″N, 90°25′15″W
		Portage	48°3′30″N, 90°35′00″W
		Kings Road	48°5′1″N, 90°46′52″W
		Unit 91	48°5′5″N, 90°49′17″W
Jack pine	Undisturbed	Dumpster[a]	48°7′31″N, 90°51′50″W
		Rotten Jack[a]	48°7′51″N, 90°51′30″W
		Larch Creek	48°8′18″N, 90°51′30″W
		Guard Station	48°7′29″N, 90°51′40″W
	Wind-disturbed	Dumpster[a]	48°7′12″N, 90°50′50″W
		Rotten Jack[a]	48°8′3″N, 90°51′10″W
		Larch Creek	48°7′30″N, 90°50′50″W
		Guard Station	48°7′32″N, 90°49′45″W
	Salvaged	Dumpster[a]	48°7′21″N, 90°51′25″W
		Rotten Jack[a]	48°7′27″N, 90°51′00″W
		Larch Creek	48°8′12″N, 90°51′25″W
		Guard Station	48°7′40″N, 90°50′00″W
	Burned	Guard Station	48°7′31″N, 90°50′30″W
		King Road	48°5′00″N, 90°48′12″W
		Up the Hill	48°4′59″N, 90°47′35″W
		Next to Up the Hill	48°5′12″N, 90°47′35″W

[a] Plots sampled in 2000–2003; remaining plots were sampled in 2001–2003.

before burning. Both salvaged and burned plots were planted with *Pinus banksiana*, *P. resinosa* Aiton, and *P. strobus* L. seedlings after the treatments. Salvaging was conducted between summer 1999 and spring 2000, whereas burning was conducted in fall 2000 and spring 2001 (Fig. 1a and b). In 2000, we sampled two plots (replicates) for each of three land-area treatment types (undisturbed, severely wind-disturbed, and salvaged) in each of the two (ABC and JP) cover types for a total of 12 plots. In 2001–2003, we sampled four plots for each of the four land-area treatment types (undisturbed, severely wind-disturbed, salvaged, and burned) in each of the two (ABC and JP) cover types for a total of 32 plots. Baited sampling (see below) was conducted on all 12 plots in 2000 and only on the 16 JP plots in 2001–2003.

2.3. Beetle sampling

Beetles were sampled with unbaited pitfall traps that consisted of a 500 ml cylindrical plastic container placed within a 1 l plastic liner (Spence and Niemelä, 1994). The liner and container were inserted in the ground so that the opening of the container was at the level of the surface of the forest floor. The smaller container contained 200 ml of propylene glycol (recreational vehicle antifreeze, Peak Co., Northbrook, IL) that killed and preserved the beetles. The trap was covered with a 100 cm^2 plywood board suspended 4 cm above the entire trap to minimize flooding and disturbance by animals. We also assessed populations of rhizophagous curculionid and scolytid beetles (reported elsewhere) in pitfall traps baited with various host-attractants, and ground beetles were caught incidentally in these traps. The baited pitfall trap design was the same as above, but included release devices with conifer attractants (kairomones for curculionids and scolytids) that were hung from the roof and placed inside the inner cup above the level of propylene glycol. Four host-attractants were used: 2% (−)-α-pinene, 2% (+)-α-pinene, 2% (−)-β-pinene (all dissolved in ethanol), and a 100% ethanol control. In 2000, the host-attractants were released from glass vials (15 ml total volume) with wicks inserted in them. In 2001 and 2002, the host-attractants were released from polyethylene bottles (15 ml total volume) (Pherotech International Inc., Delta, BC). In 2003, host-attractants were released from these polyethylene bottles with a 0.13 cm^2 hole in the side of the vial cap, and the mean (±S.E.) release rate of ethanol or its solutions was approximately 506 ± 15 mg/day. Release devices were not replaced in the summer of 2000, but were replaced in July in 2001 and 2002, and were replaced every 2 weeks in 2003.

Table 2
Attributes of the overstory of aspen/birch/conifer and jack pine stands in the Superior National Forest, Cook Co., Minnesota, USA

Stand attributes[a]	Aspen/birch/conifer[b]	Jack pine[b]
Soil pH	5.31 ± 0.05	5.02 ± 0.07
Mean age (years)	71.33 ± 3.62	75.29 ± 1.64
Total basal area (m^2/ha)	22.10 ± 8.24	25.37 ± 6.70
Basal area (m^2/ha) by species		
Aspen, *Populus tremuloides* Michx.	10.95 ± 2.98	2.33 ± 1.50
Jack pine, *Pinus banksiana* Lamb.	2.50 ± 1.85	18.17 ± 2.60
Balsam fir, *Abies balsamea* (L.) P. Mill.	2.18 ± 0.4	0.67 ± 0.33
Paper birch, *Betula papyrifera* Marsh.	5.12 ± 2.23	0.83 ± 0.37
Black spruce, *Picea mariana* (P. Mill.) B.S.P.	1.35 ± 0.78	3.37 ± 1.90

[a] Data collected between 1999 and 2002 (Gilmore et al., 2002,2005, Gilmore, unpublished data, Johnson, 2004).
[b] Data are means ± standard error.

Sampling of beetles during the summer of 2000 was preliminary. In 2000, six unbaited pitfall traps were placed on straight-line transects within each of the 12 plots (a total of 72 traps). In 2001–2003, six unbaited pitfall traps were assigned to six sample sub-plots randomly drawn from a grid of 28 sub-plots in each of the 32 plots (a total of 192 traps). In 2000, 12 baited pitfall traps with three replicates of each bait treatment were allocated randomly along two transects (six traps per transect) (a total of 144 traps). In 2001–2003, five baited pitfall traps (including an unbaited control) were assigned to five sample sub-plots randomly drawn from a grid of 28 sub-plots in each of the 16 JP plots (a total of 80 traps across only the JP cover type). In 2001–2003, baited pitfall traps were not placed in the ABC cover type.

Pitfall traps were separated by >20 m to reduce trap interactions (Digweed et al., 1995), and were placed >50 m from the plot edges to reduce edge-effects. Traps were operated from July to October in 2000 and from May to October in 2001–2003. Traps were emptied every 15–30 days in 2000, and every 15–20 days in 2001–2003. When baited pitfall traps were emptied, the inner cups and the associated baits were re-randomized on the five outer cup locations (i.e., among the five sub-plots) to account for within site variation.

Table 3
Ground beetle species caught in unbaited and baited pitfall traps in two cover types and by land-area treatment, 2000–2003, Superior National Forest, Cook Co., Minnesota, USA

Tribes	Beetle species	Aspen/birch/conifer				Jack pine				
		UD[a]	WD[a]	WD-S-L[a]	WD-P-B[a]	UD[a]	WD[a]	WD-S-L[a]	WD-P-B[a]	Totals
Notiophilini	*Notiophilus aquaticus* (L.)[b,c]	0	0	0	0	0	0	0	1	1
	Notiophilus semistriatus Say	0	0	1	0	10	3	1	1	16
Loricerini	*Loricera pilicornis pilicornis* (Fabricius)[d]	0	0	3	0	0	0	2	0	5
Carabini	*Calosoma frigidum* Kirby	120	41	17	5	4	1	2	21	211
	Carabus serratus Say	0	0	0	2	15	18	14	20	69
Cychrini	*Scaphinotus bilobus* (Say)	10	5	1	3	5	13	0	0	37
	Sphaeroderus lecontei Dejean	82	57	77	23	77	57	14	9	396
	Sphaeroderus nitidicollis brevoorti LeConte[b]	81	36	21	10	0	0	0	0	148
Trechini	*Trechus apicalis* Motschulsky	0	1	0	0	0	1	4	0	6
	Trechus crassiscapus Lindroth[b,d]	0	1	0	0	0	0	0	0	1
Bembidiini	*Bembidion grapei* Gyllenhal[d]	0	0	1	1	0	0	0	3	5
	Bembidion mutatum Gemminger and Harold[b,d]	0	0	0	1	0	0	1	1	3
	Bembidion quadrimaculatum oppositum Say	0	0	0	2	0	0	0	1	3
	Bembidion rapidum (LeConte)[d]	0	0	1	1	0	0	0	0	2
	Bembidion versicolor (LeConte)[d]	0	0	0	0	1	0	1	0	2
	Bembidion wingatei Bland[b,d]	1	0	0	0	2	0	1	0	4
	Tachyta nana kirbyi Casey[d]	0	0	0	1	0	0	0	0	1
Patrobini	*Patrobus foveocollis* (Eschscholtz)[b]	0	1	0	1	0	0	1	0	3
	Patrobus septentrionis Dejean[b,d]	0	1	0	0	0	0	0	0	1
Pterostichini	*Myas cyanescens* Dejean	0	0	0	0	53	45	17	0	115
	Poecilus lucublandus lucublandus (Say)	3	1	102	280	0	0	385	662	1433
	Pterostichus adstrictus Eschscholtz	243	150	668	1555	186	139	88	1656	4685
	Pterostichus coracinus (Newman)	176	124	200	39	813	215	253	164	1984
	Pterostichus femoralis (Kirby)[c]	0	0	0	0	0	1	0	0	1
	Pterostichus luctuosus (Dejean)[c]	0	0	0	0	0	0	2	0	2
	P. melanarius (Illiger)[b,e]	472	56	745	2622	224	11	832	5561	10,523
	Pterostichus mutus (Say)	0	0	2	36	1	0	3	110	152
	Pterostichus pensylvanicus LeConte	426	181	623	168	744	317	293	257	3,009
	Pterostichus punctatissimus (Randall)[d]	0	0	0	0	1	0	0	0	1
	Pterostichus tenuis Casey	0	0	3	0	0	2	12	0	17
Zabrini	*Amara coelebs* Hayward[b]	0	1	5	10	0	0	5	23	44
	Amara impuncticollis (Say)	0	0	2	20	0	0	0	17	39
	Amara latior (Kirby)	0	0	13	22	0	0	9	28	72
	Amara musculis (Say)[d]	0	0	0	1	0	0	0	0	1
	Amara obesa (Say)[c]	0	0	0	0	0	0	0	1	1
	Amara sinuosa (Casey)	0	0	1	0	0	0	0	1	2
	Pseudamara arenaria (LeConte)[b,d]	0	0	1	0	0	0	0	0	1
Chlaeniini	*Chlaenius sericeus sericeus* (Forster)[c]	0	0	0	0	0	0	4	0	4
Licinini	*Badister obtusus* LeConte[d]	1	0	3	0	0	0	0	0	4
Harpalini	*Bradycellus lugubris* (LeConte)[d]	0	0	0	0	0	0	0	1	1
	Bradycellus semipubescens Lindroth[b,c]	0	0	0	0	0	0	1	0	1
	Harpalus caliginosus (Fabricius)[d]	0	0	0	0	0	0	0	1	1
	Harpalus fuliginosus Duftschmid[d]	0	0	0	0	0	0	1	0	1
	Harpalus innocuus LeConte	0	0	0	7	1	2	2	35	47
	Harpalus laevipes Zetterstedt	0	0	1	24	0	0	0	49	74
	Haparlus lewisii LeConte	0	0	3	53	0	0	6	133	195
	Harpalus megacephalus LeConte	0	0	0	0	0	0	4	0	4
	Harpalus pensylvanicus (DeGeer)[d]	0	0	0	1	0	0	1	0	2
	Harpalus somnulentus Dejean	7	5	16	15	3	2	6	39	93
	Stenolophus comma (Fabricius)[d]	0	0	0	0	0	0	1	0	1

Table 3 (*Continued*)

Tribes	Beetle species	Aspen/birch/conifer				Jack pine				
		UD[a]	WD[a]	WD-S-L[a]	WD-P-B[a]	UD[a]	WD[a]	WD-S-L[a]	WD-P-B[a]	Totals
Platynini	*Agonum affine* Kirby[b,d]	0	0	0	0	0	0	1	0	1
	Agonum cupripenne Say	0	0	42	7	0	0	808	155	1,012
	Agonum cupreum Dejean[d]	0	0	0	2	0	0	0	2	4
	Agonum dilutipenne Motschulsky[d]	0	0	0	1	0	0	0	0	1
	Agonum gratiosum (Mannerheim)	1	15	20	0	0	1	2	0	39
	Agonum metallescens (LeConte)[c]	0	0	0	0	0	0	1	0	1
	Agonum muelleri (Herbst)[e]	0	0	0	0	0	0	2	1	3
	Agonum placidum (Say)	0	0	2	4	1	0	8	5	20
	Agonum retractum LeConte	41	51	49	32	23	45	8	89	338
	Agonum sordens Kirby[d]	0	1	0	2	0	0	0	0	3
	Agonum tenue (LeConte)[d]	0	0	0	0	0	1	1	0	2
	Agonum trigeminum Lindroth[b]	0	0	6	0	0	1	5	0	12
	Calathus ingratus Dejean	684	326	398	330	343	138	81	619	2,919
	Platynus decentis (Say)	69	36	66	21	14	20	45	78	349
	Platynus mannerheimii (Dejean)	1	6	15	2	0	10	1	2	37
	Platynus tenuicollis (LeConte)[d]	1	0	0	0	0	0	0	0	1
	Sericoda obsoleta (Say)	0	0	0	34	0	0	0	22	56
	Sericoda quadripunctata (DeGeer)	0	0	0	69	0	0	0	22	91
	Synuchus impunctatus (Say)	147	57	174	168	312	134	108	314	1,414
Lebiini	*Cyminidis cribricollis* Dejean	20	11	26	6	10	13	23	31	140
	Syntomus americanus (Dejean)	0	0	1	0	1	0	2	2	6
Total no. of individuals		2586	1164	3309	5581	2844	1190	3062	10,137	29,873
Total no. of species		20	23	35	39	23	24	45	38	71

[a] UD, undisturbed forest; WD, wind-disturbed forest; WD-S-L, wind-disturbed-salvage-logged forest; WD-P-B, wind-disturbed-prescribed-burned forest. Note that the prescribed-burned forest areas had also been previously salvage-logged.
[b] New state records for Minnesota (Gandhi et al., 2005).
[c] Trapped only in baited pitfall traps.
[d] Trapped only in unbaited pitfall traps.
[e] Introduced ground beetle species.

Adult ground beetles were identified by K.J.K. Gandhi by using taxonomic keys and species descriptions provided by Lindroth (1961–1969), Liebherr (1991), Noonan (1991), Downie and Arnett (1996), Liebherr and Will (1996), Bousquet (1999), and Ball and Bousquet (2000). Voucher specimens have been deposited with the University of Minnesota Insect Collection, St. Paul, MN and the California Academy of Sciences, San Francisco, CA.

2.4. Data analyses

2.4.1. Ground beetle trap catches

2.4.1.1. Unbaited pitfall traps. Trap catches of ground beetles in this study provided an indirect measure of relative abundance, i.e., abundance as a function of the activity of a given species (Spence and Niemelä, 1994; Apigian et al., 2006a,b). As in other studies, we refer to species abundance in this paper with the understanding that our trap catches reflect activity-density (Apigian et al., 2006a,b). Trap catches were standardized to 1000 trap-days [(trap catch/total number of days that traps were operational) × 1000] (Spence et al., 1996). Standardization makes an adjustment of trap catches for days when the traps were disturbed by animals or flooding, and accounts for the variable number of days when the traps were operational between the plots. Standardized trap catches were then pooled over each season to allow comparison across years.

For all analyses, statistical significance of factors was assessed at $\alpha = 0.05$. Significant terms in each final model are presented in the tables; all data were back-transformed before presentation. Unless specified, only significant results are described in Section 3. For 2000, we used two-factor analysis of variance (ANOVA) to compare beetle catches between cover types and land-area treatments (SAS, 1999–2001). For 2001–2003, we used three-factor ANOVA to compare beetle catches among years, cover types, and land-area treatments. Data were first checked for the required assumptions of constant variance and normality by using residual and normality plots. The Kolmogorov–Smirnov test was conducted on the residuals to test the null hypothesis that the data were normally distributed (SAS, 2000). Data for standardized ground beetle catches (all species pooled) in 2000 met the assumptions of normality and constant variance, whereas data for all species pooled for 2001–2003 did not meet the assumptions of normality. Consequently, data for 2001–2003 were transformed [$\ln(x + 1)$] prior to ANOVA. The Ryan–Einot–Gabriel–Welsch (REGW) test, which controls for Type I experimentwise error rate, was used for pairwise comparisons among treatment means (Day and Quinn, 1989). We conducted the same analyses on the trap catches of the 11 most frequently trapped ground beetle species (i.e., those with ≥200 individuals or ≥1% of the total ground beetle catch) in 2001–2003. Trap catches for each of these species were also transformed [$\ln(x + 1)$] prior to ANOVA.

2.4.1.2. Baited pitfall traps. Trap catches were standardized to 15 days [(trap catch/total number of days that trap was operational) × 15] as the traps were re-randomized and emptied approximately every 2 weeks. Catches from disturbed baited pitfall traps were excluded from analyses. A three-factor ANOVA was performed for the year 2000 with cover type, land-area treatment, and bait-type as factors (SAS, 1999–2001). Data for the standardized ground beetle catches in 2000 did not meet the assumptions of normality and were transformed [$\ln(x + 1)$] prior to ANOVA. Split-plot analyses of variance tests were further performed for 2001–2003 by using the PROC MIXED option in SAS (SAS, 1999–2001). The whole-plot factor was land-area treatment and the split-plot factors were bait-type and year. The least-square means approach was used for pairwise comparisons among treatment means. The Satterthwaite Approximation was used to calculate the correct degrees of freedom for the pairwise comparisons (Zar,

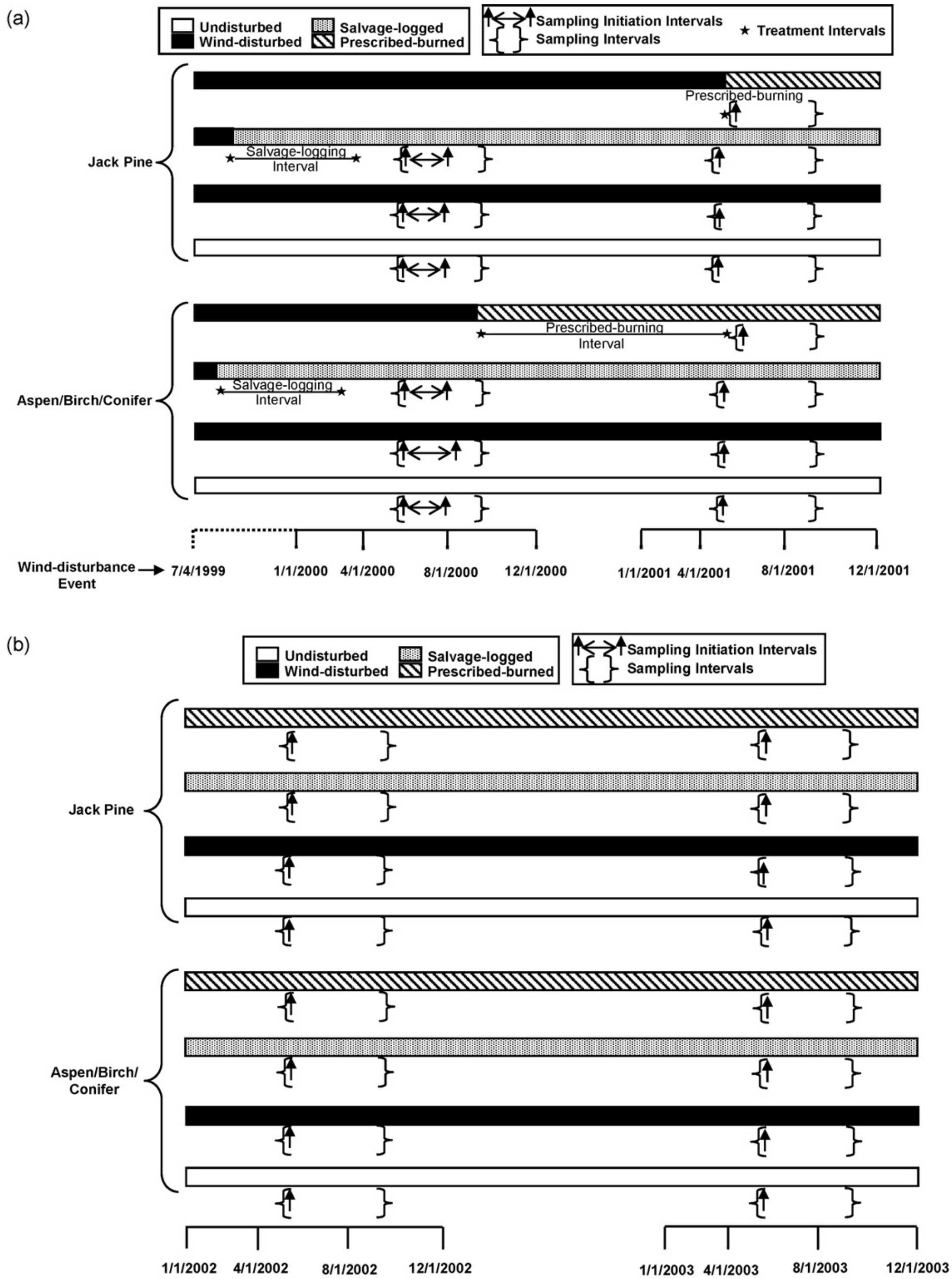

Fig. 1. Chronology of fuel-reduction treatments and beetle sampling in 1999–2001 (a) and 2002–2003 (b) relative to the wind-disturbance event on 4 July 1999.

1996). We conducted the same analyses as above on the trap catches of the eight most frequently trapped ground beetle species (i.e., those with ≥200 individuals or ≥1% of the total ground beetle catch) in 2001–2003.

2.4.2. Ground beetle species richness and diversity

Venn diagrams were used to illustrate relationships of species richness (total number of species) among cover types and land-area treatments. In the diagrams, each habitat set is represented by a circle that contains the unique numbers of species; overlapping areas depict numbers of beetle species held in common with other cover type or land-area treatment combinations (Langbehn et al., 1972). Venn diagrams were constructed for species richness as follows: (1) 2000–2003 unbaited pitfall traps in the ABC and JP cover types; (2) 2001–2003 unbaited pitfall traps in the ABC and JP cover types, respectively, among groups of three of the four land-area treatments; and (3) 2001–2003 baited pitfall traps in the JP cover type, among groups of three of the four land-area treatments.

Rarefaction indices were used to estimate mean ground beetle diversity (richness and evenness) from the unbaited pitfall traps from 2001 to 2003 in each combination of cover type and land-area treatment. This technique accounts for differences in trapping effort among habitats and is ideal for catches with variable trapping intervals (Magurran, 1988, software developed by Holland, 2003). Simpson's index was also used to assess species diversity and dominance (Magurran, 1988; McCune and Mefford, 1999). The reciprocal form of the dominance measure was used to ensure that species diversity increased and dominance decreased with an increasing index value (Magurran, 1988).

2.4.3. Ground beetle species composition

Ground beetle species compositions for each cover type and land-area treatment for 2000–2003 were compared by constructing dendrograms with a similarity percentage scale. Standardized mean beetle catches within each treatment-type were analyzed by using the Bray-Curtis distance analysis with the group average clustering option (McCune and Mefford, 1999; McCune and Grace, 2002). Cluster analyses were performed for the ground beetle assemblages in the cover type-land-area treatment combinations in 2000–2003 for the unbaited and baited pitfall traps with and without the numerically dominant *Pterostichus melanarius* (Illiger).

3. Results

During the summers of 2000–2003, 5704 pitfall trap samples yielded a total of 29,873 ground beetle adults, representing 71 species, 27 genera, and 14 tribes (Table 3). Sixty species were rare (each <1% of the total ground beetle catch); eight species were common (1–10% of total ground beetle catch); and three species were abundant (>10% of total ground beetle catch). Twenty-three ground beetle species were caught exclusively in unbaited pitfall traps, whereas five species were caught exclusively in baited pitfall traps.

Four species made up 72% of the total catch. *P. melanarius* was the most abundant ground beetle (35% of the total catch) followed by *Pterostichus adstrictus* Eschscholtz (16%), *P. pensylvanicus* LeConte (11%), and *Calathus ingratus* Dejean (10%). Thirteen species, including *Agonum affine* Kirby, *Ag. trigeminum* Lindroth, *Amara coelebs* Hayward, *Bembidion mutatum* Gemminger and Harold, *B. wingatei* Bland, *Bradycellus semipubescens* Lindroth, *Notiophilus aquaticus* (L.), *Patrobus foveocollis* (Eschscholtz), *Pa. septentrionis* Dejean, *P. melanarius*, *Pseudamara arenaria* (LeConte), *Sphaeroderus nitidicollis brevoorti* LeConte, and *Trechus crassiscapus* Lindroth, caught in this study are new state records for Minnesota (Gilmore et al., 2002; Gandhi et al., 2005). In addition, *Ag. muelleri* (Herbst) and *P. melanarius* are introduced ground beetle species from Europe (Lindroth, 1961–1969).

3.1. Ground beetle trap catches

3.1.1. Unbaited pitfall traps

The two-way ANOVA for pooled trap catches of all ground beetle species for the year 2000 showed that none of the main factors or interactions was significant in the model (Table 4). The three-way ANOVA and the REGW posthoc tests for all ground beetle species for the years 2001–2003 showed that 34% more beetles were caught in the ABC than in the JP cover type (Fig. 2, Table 4). Significantly more beetles were caught in the burned forest plots than in the other land-area treatments; the lowest catches were in the wind-disturbed forest plots (Fig. 2).

In 2001–2003, 11 ground beetle species in order of decreasing catches in unbaited pitfall traps included *P. melanarius*, *P. adstrictus*, *C. ingratus*, *P. pensylvanicus*, *P. coracinus* (Newman), *Synuchus impunctatus* (Say), *Poecilus lucublandus lucublandus* (Say), *Sphaeroderus lecontei* Dejean, *Platynus decentis* (Say), *Ag. cupripenne* Say, and *Ag. retractum* LeConte (Fig. 3, Tables 3 and 5).

The following main effects were significant in the species-level analyses (Table 4): (1) year for *P. coracinus* and *S. impunctatus*; (2) cover type for *Ag. retractum* and *Sp. lecontei*; and (3) land-area treatment for *Ag. cupripenne*, *P. coracinus*, *P. pensylvanicus*, *Sp. lecontei*, and *S. impunctatus*. The responses of these species (Table 5) can be described as: (1) more *S. impunctatus* were caught in 2002 and 2003 than in 2001; (2) more *Ag. retractum* and *Sp. lecontei* were caught in the ABC than in the JP cover type; (3) *Ag. cupripenne* was only caught in salvaged and burned forest plots; (4) more *P. coracinus*, *P. pensylvanicus*, and *Sp. lecontei* were caught in undisturbed forest plots than in the other land-area treatments; and (5) more *S. impunctatus* were caught in the burned than in the wind-disturbed and salvaged plots and in the undisturbed and salvaged than in the wind-disturbed forest plots.

The following interactions were significant in the species-level analyses (Table 4): (1) year and cover type for *C. ingratus* and *P.*

Table 4
ANOVA model for unbaited pitfall trap catches of all ground beetle species pooled in 2000 and 2001–2003, and of eleven common and abundant species in 2001–2003 with year (YR), cover type (CT), land-area treatment (LT), and their interactions as factors, Superior National Forest, Cook Co., Minnesota, USA

Source	YR	CT	LT	YR × CT	YR × LT	CT × LT	YR × CT × LT
Total trap catches 2000[a]	NA[b]	NS[b]	NS[b]	NA[b]	NA[b]	NS[b]	NA[b]
Total trap catches 2001–2003[c]	NS[b]	$14.34_{1,95}$; <0.001	$21.32_{3,95}$; <0.001	NS[b]	NS[b]	NS[b]	NS[b]
Ag. cupripenne[d]	NS[b]	NS[b]	$10.24_{3,95}$; <0.001	NS[b]	NS[b]	NS[b]	NS[b]
Agonum retractum[d]	NS[b]	$23.25_{1,95}$; <0.001	NS[b]	NS[b]	NS[b]	NS[b]	NS[b]
Calathus ingratus[d]	NS[b]	$28.7_{1,95}$; <0.001	$8.17_{3,95}$; <0.001	$5.8_{2,95}$; 0.004	NS[b]	$3.08_{3,95}$; 0.032	NS[b]
Platynus decentis[d]	NS[b]	$10.32_{1,95}$; 0.002	NS[b]	NS[b]	NS[b]	$3.03_{3,95}$; 0.034	NS[b]
Poecilus l. lucublandus[d]	$5.32_{2,95}$; 0.007	NS[b]	$41.94_{3,95}$; <0.001	NS[b]	$2.61_{6,95}$; 0.023	NS[b]	NS[b]
Pterostichus adstrictus[d]	NS[b]	$33.6_{1,95}$; <0.001	$26.5_{3,95}$; <0.001	NS[b]	NS[b]	$2.83_{3,95}$; 0.043	NS[b]
P. coracinus[d]	$3.58_{2,95}$; 0.032	NS[b]	$8.01_{3,95}$; <0.001	NS[b]	NS[b]	NS[b]	NS[b]
P. melanarius[d]	NS[b]	NS[b]	$23_{3,95}$; <0.001	NS[b]	NS[b]	$3.13_{3,95}$; 0.03	NS[b]
Pterostichus pensylvanicus[d]	$3.32_{2,95}$; 0.041	$4.89_{1,95}$; 0.03	$5.72_{3,95}$; 0.001	$3.58_{2,95}$; 0.032	NS[b]	NS[b]	NS[b]
Sp. lecontei[d]	NS[b]	$24.93_{1,95}$; <0.001	$8.63_{3,95}$; <0.001	NS[b]	NS[b]	NS[b]	NS[b]
Synuchus impunctatus[d]	$7_{2,95}$; 0.002	NS[b]	$10.42_{3,95}$; <0.001	NS[b]	NS[b]	NS[b]	NS[b]

For each table entry, the first number is the *F*-value with degrees of freedom as subscripts; the second number is the *P*-value.

[a] The ANOVA model was as follows: $Y_{ij} = CT_i + LT_j + (CT \times LT)_{ij} + \varepsilon_{ij}$ where Y_{ij} is the observed trap catch for cover type and land-area treatment; *i*, *j* are the numbers of levels for each factor; and ε_{ij} is the error term (unaccounted variation in the model).

[b] NA = non-applicable in the model; NS = non-significant factor in the model.

[c] The ANOVA model was as follows: $Y_{ijk} = YR_i + CT_j + LT_k + (YR \times CT)_{ij} + (YR \times LT)_{ik} + (CT \times LT)_{jk} + (YR \times CT \times LT)_{ijk} + \varepsilon_{ijk}$ where Y_{ijk} is the observed trap catch for year, cover type and land-area treatment; *i*, *j*, *k* are the numbers of levels for each factor; and ε_{ijk} is the error term (unaccounted variation in the model).

[d] Data from 2001 to 2003.

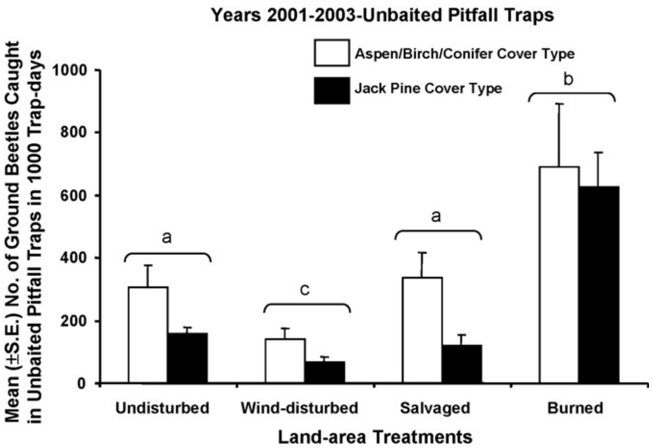

Fig. 2. Mean (+S.E.) number of ground beetles per 1000 trap-days caught in unbaited pitfall traps during 2001–2003 in the undisturbed, wind-disturbed, salvaged, and burned plots in the aspen/birch/conifer and jack pine cover types.

pensylvanicus; (2) year and land-area treatment for *Po. l. lucublandus*; and (3) cover type and land-area treatment for *C. ingratus*, *Pl. decentis*, *P. adstrictus*, and *P. melanarius*. All of the significant interaction graphs are presented as Supplementary data. The responses of these species (Table 5) interpreted in the context of the interactions can be described as: (1) more *C. ingratus* in the ABC cover type in all land-area treatments except the burned sites in 2001 and 2003; (2) more *P. pensylvanicus* in the ABC cover type in 2002 and 2003 than in 2001; (3) *Po. l. lucublandus* was absent in the undisturbed and wind-disturbed forest plots, except in 2002, and was caught in low numbers in burned plots in 2001 relative to 2002 and 2003; (4) more *Pl. decentis* in the ABC cover type in the undisturbed and wind-disturbed sites, but more in the JP cover type in salvaged and burned sites; (5) more *P. adstrictus* in the ABC cover type in all land-area treatments; and (6) more *P. melanarius* caught in burned areas of both cover types, but also more were caught in undisturbed areas of the ABC than the JP cover type (Fig. 3).

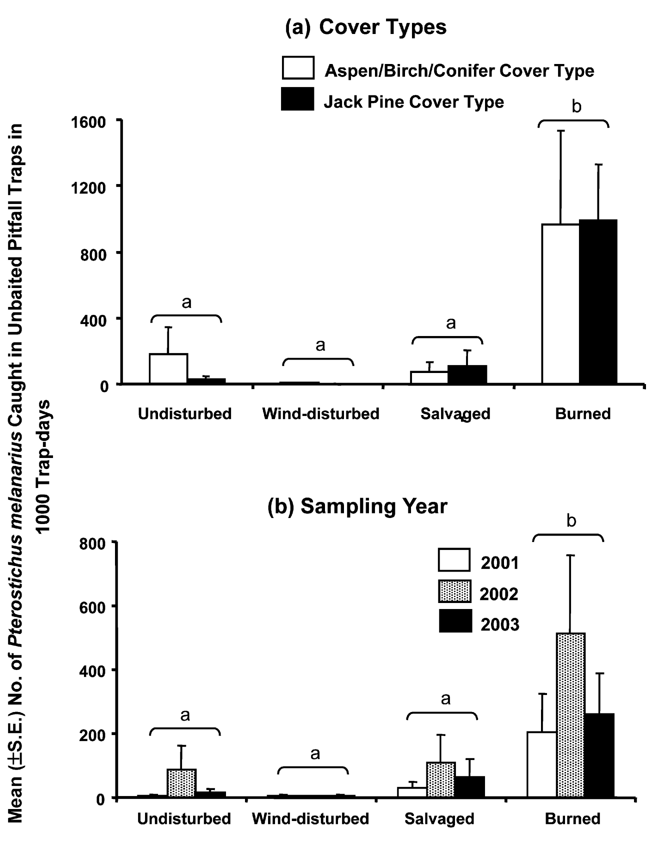

Fig. 3. Mean (+S.E.) number of *Pterostichus melanarius* per 1000 trap-days caught in unbaited pitfall traps during 2001–2003 in the undisturbed, wind-disturbed, salvaged, and burned plots in the aspen/birch/conifer and jack pine cover types.

3.1.2. Baited pitfall traps

The three-way ANOVA for all ground beetle species in baited pitfall traps for the year 2000 revealed an interaction between cover type and land-area treatment (Table 6, footnote b). All of the significant interaction graphs are presented as Supplementary data. Twenty-five percent more beetles were caught in the JP undisturbed forests than in other land-area treatments in the JP cover type (data not shown). Twenty-five percent more beetles were caught in the ABC salvaged forests than in the other land-area treatments in the ABC cover type (data not shown). The split-plot ANOVA for all ground beetle species for 2001–2003 revealed a significant interaction between land-area treatment and year (Table 6). In 2002 and 2003, more beetles were caught in the burned forests as compared to the wind-disturbed forests (up to 1500%) (Fig. 4). Bait was never significant as a main effect or as an interaction in the models, whether the species were pooled or analyzed alone (Table 6).

In 2001–2003, eight species in the order of decreasing catches in baited pitfall traps included *P. melanarius*, *P. adstrictus*, *Ag. cupripenne*, *Po. l. lucublandus*, *P. pensylvanicus*, *P. coracinus*, *C. ingratus*, and *S. impunctatus* (Fig. 5, Tables 3 and 7). These eight species were also among the 11 most abundant species caught in unbaited traps (Tables 3 and 5).

The following main effects were significant in the species level analyses (Table 6): (1) land-area treatment for *Ag. cupripenne*, *P. coracinus*, and *P. pensylvanicus* and (2) year for *P. pensylvanicus*. The responses of these species (Table 7) can be described as: (1) more *Ag. cupripenne* caught in the salvaged than in the undisturbed, wind-disturbed, or burned sites where they were nearly absent (least-square means comparison); (2) more *P. coracinus* caught in the undisturbed than in the burned sites (least-square means comparison); (3) more *P. pensylvanicus* caught in the undisturbed sites than in the rest of the land-area treatments (least-square means comparison) and the response was higher in 2001 and 2002, than 2003 (least-square means comparison).

The interaction of land-area treatment and year was significant in the species-level analyses for *C. ingratus*, *Po. l. lucublandus*, *P. adstrictus*, *P. melanarius*, and *S. impunctatus* (Table 6). All of the significant interaction graphs are presented as Supplementary data. The responses of these species (Table 7) interpreted in the context of the interactions can be described as: (1) more *C. ingratus*, *P. adstrictus* and *S. impunctatus* were caught in the burned sites than in the other land-area treatments in 2002 and 2003, but not in 2001; (2) *Po. l. lucublandus* was not trapped in the undisturbed or wind-disturbed sites in any year, and more were trapped in the burned sites than the salvaged sites in 2003, but not in 2001 or 2002; and (3) more *P. melanarius* were caught in the burned sites than the other land-area treatments during all three years, but more were caught in the salvaged sites in 2002 and 2003 than in the undisturbed and wind-disturbed sites (Fig. 5).

3.2. Ground beetle species richness and diversity

3.2.1. Unbaited pitfall traps

A comparison of total ground beetle species richness between ABC and JP forests from 2000 to 2003 revealed that slightly more

Table 5
Mean (±S.E.) standardized unbaited pitfall trap catches (1000 trap-days) of all ground beetle species pooled in 2000, and of ten common and abundant species[a] in 2001–2003 by year, cover type, and land-area treatment, Superior National Forest, Cook Co., Minnesota, USA

Species	Year	Cover type[b]	Undisturbed	Wind-disturbed	Salvaged	Burned	Totals
Total catches	2000[c]	ABC	57.28 ± 10.49	63.3 ± 4.47	353.44 ± 182.96	Not sampled	474.02 ± 197.92
		JP	169.41 ± 35	79.55 ± 70.78	109.2 ± 29.87	Not sampled	358.16 ± 135.65
Ag. cupripenne	2001[d]	ABC	0	0	2.88 ± 1.66	0.37 ± .04	3.25 ± 1.7
		JP	0	0	5.48 ± 4.52	0.74 ± 0.43	6.22 ± 4.95
	2002[d]	ABC	0	0	2.19 ± 0.93	1.81 ± 1.08	4 ± 2.01
		JP	0	0	30.48 ± 28.46	4.7 ± 1.06	35.18 ± 29.52
	2003[d]	ABC	0	0	10.81 ± 9.61	0.39 ± 0.39	11.2 ± 10
		JP	0	0	0.58 ± 0.58	37.66 ± 36.46	38.24 ± 37.04
Agonum retractum	2001[d]	ABC	2.36 ± 0.68	6.63 ± 2.42	4.02 ± 0.75	2.12 ± 1.28	15.13 ± 5.13
		JP	1.08 ± 1.08	1.54 ± 1.1	0	1.8 ± 0.9	4.42 ± 3.08
	2002[d]	ABC	4.28 ± 3.78	5.13 ± 2.6	9.15 ± 3.74	7.17 ± 2.9	25.73 ± 13.02
		JP	0	0.39 ± 0.39	0.39 ± 0.39	7.11 ± 3.2	7.89 ± 3.98
	2003[d]	ABC	8.46 ± 3.03	7.02 ± 1.57	3.62 ± 3.07	2.83 ± 1.67	21.93 ± 9.34
		JP	2.24 ± 0.87	0.42 ± 0.42	2.4 ± 1.84	4.61 ± 4.61	9.67 ± 7.74
Calathus ingratus	2001[d]	ABC	59.29 ± 41.47	12.53 ± 5.15	25.18 ± 13.55	27.96 ± 21.3	124.96 ± 81.47
		JP	10.40 ± 3.86	5.68 ± 3.2	3.67 ± 2.65	37.24 ± 11.35	56.99 ± 21.06
	2002[d]	ABC	133.10 ± 42.04	46.69 ± 9.57	99.85 ± 41.84	48.36 ± 12.34	328 ± 105.79
		JP	16.38 ± 9.56	5.34 ± 4.84	2.33 ± 0.99	36.92 ± 22.95	60.97 ± 38.34
	2003[d]	ABC	51.75 ± 16.92	77.85 ± 58.81	15.59 ± 10.11	49 ± 15.7	194.19 ± 101.54
		JP	37.64 ± 9.13	10.17	16.55 ± 11.98	59.77 ± 29.46	123.96 ± 50.57
Platynus decentis	2001[d]	ABC	6.87 ± 3.66	7.33 ± 3.99	9.82 ± 6.58	2.82 ± 1.49	26.84 ± 15.72
		JP	1.03 ± 1.03	0.74 ± 0.74	1.05 ± 1.05	2.88 ± 1.76	5.7 ± 4.58
	2002[d]	ABC	16.19 ± 5.94	3.91 ± 2.58	8.05 ± 4.3	4.38 ± 2.92	32.53 ± 15.74
		JP	0.4 ± 0.4	1.18 ± 0.74	2.32 ± 1	11.7 ± 10.67	15.6 ± 12.81
	2003[d]	ABC	2.87 ± 1.2	2.78 ± 1.78	0.8 ± 0.8	0.4 ± 0.4	6.85 ± 4.18
		JP	0	2.77 ± 2.25	5.44 ± 5.44	2.76 ± 1.2	10.97 ± 8.89
Poecilus l. lucublandus	2001[d]	ABC	0	0	2.65 ± 1.04	3.48 ± 1.65	6.13 ± 2.69
		JP	0	0	10.59 ± 6.48	2.2 ± 0.73	12.79 ± 7.21
	2002[d]	ABC	1.66 ± 1.66	0.39 ± 0.39	11.13 ± 5.39	37.12 ± 23.02	50.3 ± 30.46
		JP	0	0	11.97 ± 6.94	16.9 ± 5.19	28.87 ± 12.13
	2003[d]	ABC	0	0	25.15 ± 14.59	65.77 ± 40.97	90.92 ± 55.56
		JP	0	0	7.86 ± 4.2	86.02 ± 42.52	93.88 ± 46.72
Pterostichus adstrictus	2001[d]	ABC	37.64 ± 20.99	14.92 ± 4.54	48.31 ± 26.82	97.91 ± 20.21	198.78 ± 72.56
		JP	9.04 ± 6.24	14.35 ± 4.29	3.63 ± 2.38	52.43 ± 13.78	79.45 ± 26.69
	2002[d]	ABC	33.66 ± 9.17	17.04 ± 5.48	122.52 ± 92.02	344.92 ± 180.49	518.14 ± 289.16
		JP	8.87 ± 7.84	6.81 ± 1.95	1.16 ± 0.74	157.79 ± 56.69	174.63 ± 67.22
	2003[d]	ABC	12.6 ± 4.06	25.08 ± 9.73	28.6 ± 15.04	133.32 ± 48.62	199.6 ± 77.45
		JP	11.73 ± 8.93	4.49 ± 2.17	27.37 ± 26.15	97.6 ± 39.44	141.19 ± 76.69
P. coracinus	2001[d]	ABC	12.98 ± 4.38	11.89 ± 5.51	20.86 ± 16.67	6.97 ± 2.61	52.7 ± 29.17
		JP	45.25 ± 21.72	21.06 ± 13.15	12.9 ± 3.34	16.86 ± 5.07	96.07 ± 43.28
	2002[d]	ABC	27.72 ± 7.5	7.06 ± 1.48	19.49 ± 15.56	4.09 ± 0.66	58.36 ± 25.2
		JP	46.18 ± 21.16	13.68 ± 7.89	7.4 ± 1.62	21.52 ± 6.76	88.78 ± 37.43
	2003[d]	ABC	16.97 ± 6.25	12.47 ± 5.96	1.24 ± 0.77	3.97 ± 2.61	34.65 ± 15.59
		JP	59.26 ± 25.62	11.19 ± 6.48	6.98 ± 4.20	1.37 ± 0.46	78.8 ± 36.76
Pterost. pensylvanicus	2001[d]	ABC	51.52 ± 16.95	11.84 ± 5.43	62.37 ± 24.58	10.4 ± 2.80	136.13 ± 46.96
		JP	52.76 ± 15.37	26.77 ± 13.41	18.4 ± 5.92	34.44 ± 7.65	132.37 ± 42.35
	2002[d]	ABC	55.3 ± 8.12	24.72 ± 9.68	91.63 ± 13.59	41.46 ± 9.49	213.11 ± 40.88
		JP	33.48 ± 9.09	15.63 ± 7.82	15.91 ± 4.08	18 ± 8.17	83.02 ± 29.16
	2003[d]	ABC	43.83 ± 16.08	29.63 ± 5.37	25.59 ± 12.53	11.67 ± 5.52	110.72 ± 39.5
		JP	29 ± 7.95	15.7 ± 7.75	11.16 ± 5.64	10.46 ± 4.65	66.32 ± 25.99
Sp. lecontei	2001[d]	ABC	7.91 ± 1.44	2.62 ± 2.18	8.19 ± 6.46	1.37 ± 0.56	20.09 ± 10.64
		JP	6.04 ± 2.47	2.68 ± 1.13	0.35 ± 0.35	0	9.07 ± 3.95
	2002[d]	ABC	10.21 ± 1.13	4.78 ± 2.21	7.33 ± 3.13	4.87 ± 2.92	27.19 ± 9.39
		JP	3.14 ± 1.29	1.18 ± 0.74	1.17 ± 0.74	1.19 ± 0.75	6.68 ± 3.52
	2003[d]	ABC	9.07 ± 2.13	9.01 ± 1.5	5.61 ± 4.03	2.54 ± 0.39	26.23 ± 8.05
		JP	4.51 ± 1.94	5.38 ± 3.88	1.32 ± 0.88	1.38 ± 1.38	23.68 ± 8.08
Synuchus impunctatus	2001[d]	ABC	7.02 ± 1.66	0	8.17 ± 5.37	10.02 ± 6.57	25.21 ± 13.6
		JP	14.06 ± 5.1	2.73 ± 2.23	3.34 ± 1.14	8.08 ± 3.53	28.21 ± 12
	2002[d]	ABC	22.49 ± 6.8	7.06 ± 1.34	29.11 ± 14.73	24.75 ± 13.11	83.41 ± 35.98
		JP	14.88 ± 7.27	1.21 ± 0.79	4.24 ± 2.63	23.81 ± 5.58	44.14 ± 16.27
	2003[d]	ABC	14.9 ± 5.67	12.37 ± 7.06	10.38 ± 4.57	29.72 ± 1.26	67.37 ± 18.56
		JP	17.38 ± 8.9	6.73 ± 3.95	6.62 ± 2.88	30.92 ± 12.36	61.65 ± 28.09

[a] Results for *P. melanarius* are presented graphically in Fig. 3.
[b] ABC-aspen/birch/conifer cover type; JP-jack pine cover type.
[c] $N = 6$ per cover type; $N = 2$ per treatment by cover type.
[d] $N = 16$ per cover type; $N = 4$ per treatment by cover type.

Table 6
ANOVA model for baited pitfall trap catches of all ground beetle species pooled in 2000 and 2001–2003 and of eight common and abundant species in 2001–2003 with land-area treatment (LT), bait[a] (BT), year (YR), and their interactions as factors, Superior National Forest, Cook Co., Minnesota, USA

Source	LT	BT	YR	LT × BT	LT × YR	BT × YR	LT × BT × YR
Total trap catches 2000[b]	NS[c]	NS[c]	NA[c]	NS[c]	NA[c]	NA[c]	NA[c]
Total trap catches 2001–2003[d]	$108.01_{3,1523}$; <0.001	NS[c]	$35.03_{2,1523}$; <0.001	NS[c]	$25.51_{6,1523}$; <0.001	NS[c]	NS[c]
Ag. cupripenne[e]	$21.71_{3,1523}$; <0.001	NS[c]	NS[c]	NS[c]	NS[c]	NS[c]	NS[c]
Calathus ingratus[e]	$25.91_{3,1523}$; <0.001	NS[c]	$24.04_{2,1523}$; <0.001	NS[c]	$5.98_{6,1523}$; <0.001	NS[c]	NS[c]
Poecilus l. lucublandus[e]	$38.38_{3,1523}$; <0.001	NS[c]	$27.26_{2,1523}$; <0.001	NS[c]	$17.38_{6,1523}$; <0.001	NS[c]	NS[c]
Pterostichus adstrictus[e]	$150.13_{3,1523}$; <0.001	NS[c]	$19.58_{2,1523}$; <0.001	NS[c]	$23.57_{6,1523}$; <0.001	NS[c]	NS[c]
P. coracinus[e]	$25.68_{3,1523}$; <0.001	NS[c]	NS[c]	NS[c]	NS[c]	NS[c]	NS[c]
P. melanarius[e]	$86.67_{3,1523}$; <0.001	NS[c]	$27.1_{2,1523}$; <0.001	NS[c]	$19.81_{6,1523}$; <0.001	NS[c]	NS[c]
Pterostichus pensylvanicus[e]	$15.36_{3,1523}$; <0.001	NS[c]	$3.39_{2,1523}$; 0.034	NS[c]	NS[c]	NS[c]	NS[c]
Synuchus impunctatus[e]	$10.02_{3,1523}$; <0.001	NS[c]	$6.9_{2,1523}$; 0.001	NS[c]	$4.52_{6,1523}$; <0.001	NS[c]	NS[c]

For each table entry, the first number is the *F*-value with degrees of freedom as subscripts; the second number is the *P*-value.
[a] Pinenes were purchased from Sigma–Aldrich (St. Louis, MO) and all had chemical purities of ≥99%, and enantiomeric purities of >98%. Ethanol was purchased from Aaper Alcohol Co. (Shelbyville, KY) and had a chemical purity of >99.95%. Mean (±S.E.) (*N* = 16 and 4 per treatment) release rates for 15 days for each of the semiochemical blends in 2003 were: (1) 2% (−)-α-pinene in ethanol: 7.98 ± 0.23 g; (2) 2% (±)-α-pinene in ethanol: 7.64 ± 0.26 g; (3) 2% (−)-β-pinene in ethanol: 7.24 ± 0.20 g; and (4) 100% ethanol: 7.48 ± 0.20 g. This corresponds to mean (±S.E.) (*N* = 16 and 4 per treatment) release rates for 15 days for each of the pinenes as: (1) 2% (−)-α-pinene in ethanol: 160 ± 5 mg; (2) 2% (+)-α-pinene in ethanol: 153 ± 5 mg; (3) 2% (−)-β-pinene in ethanol: 145 ± 4 mg.
[b] The ANOVA model was as follows: $Y_{ijk} = CT_i + LT_j + BT_k + (CT \times LT)_{ij} + (CT \times BT)_{ik} + (LT \times BT)_{jk} + (CT \times LT \times BT)_{ijk} + \varepsilon_{ijk}$ where Y_{ijk} is the observed trap catch for cover type, land-area treatment and bait-type; *i*, *j*, *k* are the numbers of levels for each factor; and ε_{ijk} is the error term (unaccounted variation in the model). CT was non-significant but CT × LT was significant ($F = 6.01_{2,47}$, $P = 0.005$).
[c] NA = non-applicable in the model; NS = non-significant factor in the model.
[d] The ANOVA model was as follows: $Y_{ijk} = LT_i + \eta_i + BT_j + (LT \times BT)_{ij} + YR_k + (LT \times YR)_{ik} + (BT \times YR)_{jk} + (LT \times BT \times YR)_{ikj} + \varepsilon_{ijk}$ where Y_{ijk} is the observed trap catch for land-area treatment, bait-type and year; *i*, *j*, *k* are the numbers of levels for each factor; η_i is the whole-plot level random error term; and ε_{ijk} is the split-plot level random error term.
[e] Data from 2001 to 2003.

unique species were present in the ABC than in the JP cover type (Fig. 6). Seventy eight percent of the species were common to both cover types. A comparison of species richness from trap catches pooled over 2001–2003 among land-area treatments in the ABC cover type (Fig. 7a) and in the JP cover type (Fig. 7b) revealed that the salvaged and burned forests contained both the highest numbers and the most unique ground beetle species. Only 31–33% and 26–28% of the species were shared among the four land-area treatments in the ABC and JP cover types, respectively. The trends for greater species richness in the salvaged and burned forest sites were driven by the rarer species, with the exceptions of *Ag. cupripenne* and *Po. l. lucublandus*, which were frequently trapped species unique to the salvaged and burned JP sites (in both unbaited and baited traps, see below).

Rarefaction analyses of ground beetle trap catches from 2001 to 2003 showed that at a sub-sample size of 550 individuals, the JP salvaged forests had the highest estimated mean species diversity with the steepest species accumulation curve (Fig. 8). This was followed by the ABC salvaged, ABC burned, JP burned, JP wind-disturbed, and ABC wind-disturbed forests. The lowest estimated mean species diversity at this sub-sample size was observed in the JP and ABC undisturbed forests with 45% lower species diversity from the salvaged and burned sites. The burned forests, especially in the ABC cover type seemed to accumulate the most species with increasing sub-sample sizes. Simpson's diversity indices from unbaited trap catches in the ABC cover type indicated that the greatest ground beetle species diversity was in the burned forests followed by relatively similar indices for the undisturbed, wind-disturbed, and salvaged forests (Table 8). Simpson's diversity indices from unbaited trap catches in the JP cover type also indicated that the greatest ground beetle species diversity was in the burned forests (Table 8).

3.2.2. Baited pitfall traps

A comparison of ground beetle species richness among land-area treatments in the JP cover type in 2001–2003 revealed that the salvaged and burned forests contained both the highest numbers and the most unique species (Fig. 9). Only 30–37% of the species

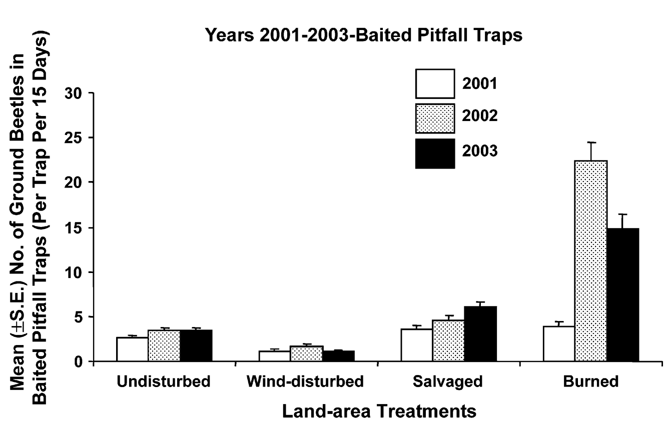

Fig. 4. Mean (+S.E.) number of ground beetles per 15 trap-days caught in baited pitfall traps during 2001–2003 in the undisturbed, wind-disturbed, salvaged, and burned plots in the jack pine cover type.

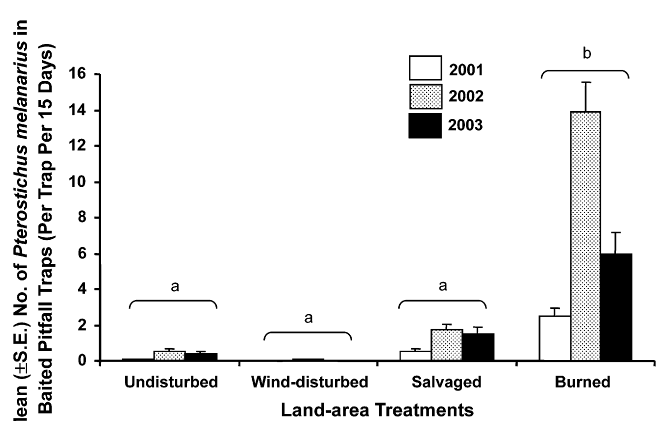

Fig. 5. Mean (+S.E.) number of *P. melanarius* per 15 trap-days caught in baited pitfall traps during 2001–2003 in the undisturbed, wind-disturbed, salvaged, and burned plots in the aspen/birch/conifer and jack pine cover types.

Table 7
Mean (±S.E.) standardized baited pitfall trap catches (15 days) of all ground beetle species pooled in 2000, and of eight common and abundant species[a] in 2001–2003 by year and land-area treatment in *Pinus banksiana* (JP) forest sites, Superior National Forest, Cook Co., Minnesota, USA

Species	Year	Undisturbed	Wind-disturbed	Salvaged	Burned	Totals
Total catches	2000[b]	240.64 ± 69.69	161.24 ± 35.12	267.38 ± 55.92	Not sampled	669.16 ± 160.73
Ag. cupripenne	2001[c]	0	0	1.18 ± 0.29	0	1.18 ± 0.29
	2002[c]	0	0	1.01 ± 0.27	0.10 ± 0.03	2.76 ± 0.3
	2003[c]	0	0	2.45 ± 0.92	0.31 ± 0.12	2.76 ± 1.04
Calathus ingratus	2001[c]	0.12	0.14 ± 0.05	0.04 ± 0.02	0.19 ± 0.05	0.49 ± 0.12
	2002[c]	0.3 ± 0.07	0.24 ± 0.07	0.09 ± 0.03	0.87 ± 0.14	1.5 ± 0.31
	2003[c]	0.81 ± 0.18	0.2 ± 0.06	0.22 ± 0.1	1.27 ± 0.22	2.5 ± 0.56
Poecilus l. lucublandus	2001[c]	0	0	0.35 ± 0.08	0.07 ± 0.03	0.42 ± 0.11
	2002[c]	0	0	0.58 ± 0.11	0.65 ± 0.12	1.23 ± 0.23
	2003[c]	0	0	0.88 ± 0.23	2.68 ± 0.5	3.56 ± 0.73
Pterostichus adstrictus	2001[c]	0.30	0.24 ± 0.09	0.18 ± 0.05	0.51 ± 0.07	1.23 ± 0.21
	2002[c]	0.34 ± 0.09	0.22 ± 0.09	0.09 ± 0.03	4.30 ± 0.62	4.95 ± 0.83
	2003[c]	0.21 ± 0.07	0.08 ± 0.03	0.04 ± 0.02	2.08 ± 0.34	2.41 ± 0.46
P. coracinus	2001[c]	0.78 ± 0.28	0.14 ± 0.05	0.47 ± 0.09	0.07 ± 0.02	1.46 ± 0.44
	2002[c]	0.92 ± 0.24	0.21 ± 0.06	0.47 ± 0.08	0.27 ± 0.05	1.87 ± 0.43
	2003[c]	0.79 ± 0.16	0.18 ± 0.08	0.14 ± 0.04	0.10 ± 0.04	1.21 ± 0.32
P. pensylvanicus	2001[c]	0.86	0.42 ± 0.12	0.40 ± 0.1	0.12 ± 0.03	1.8 ± 0.25
	2002[c]	0.91 ± 0.16	0.47 ± 0.11	0.35 ± 0.07	0.32 ± 0.08	2.05 ± 0.42
	2003[c]	0.54 ± 0.09	0.11 ± 0.05	0.35 ± 0.1	0.28 ± 0.06	1.28 ± 0.3
Synuchus impunctatus	2001[c]	0.28	0.06 ± 0.03	0.17 ± 0.08	0.07 ± 0.03	0.58 ± 0.14
	2002[c]	0.24 ± 0.06	0.17 ± 0.05	0.08 ± 0.03	0.59 ± 0.11	1.08 ± 0.25
	2003[c]	0.31 ± 0.07	0.19 ± 0.07	0.22 ± 0.08	0.61 ± 0.12	1.33 ± 0.34

[a] Results for *P. melanarius* are presented graphically in Fig. 5.
[b] $N = 6$; $N = 2$ per treatment by cover type. Data for 2000 includes catches from aspen/birch/conifer and jack pine cover types. These catches were standardized to 1000 trap-days.
[c] $N = 16$; $N = 4$ per treatment by cover type.

were shared among the JP undisturbed, wind-disturbed, salvaged, and burned forests. Simpson's diversity indices from baited trap catches in the JP cover type indicated that the greatest species diversity was in the burned forests (Table 8).

3.3. Ground beetle species composition

3.3.1. Unbaited pitfall traps

Cluster analysis of ground beetle species composition from unbaited traps among cover type-land-area treatment combinations revealed that the treatments clustered primarily into two distinct groups: (1) ABC and JP burned forests; and (2) ABC and JP undisturbed, wind-disturbed, and salvaged forests (Fig. 10). There was a 100% similarity in species composition between the ABC and JP burned forests, and a 95% similarity in species composition

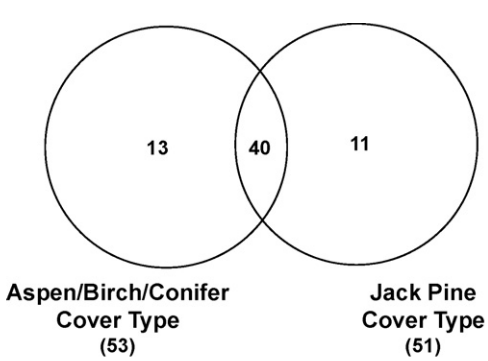

Fig. 6. Venn diagram depicting the total number of ground beetle species trapped in unbaited pitfall traps in 2000–2003, and shared by or unique to the aspen/birch/conifer and jack pine cover types. Values in parentheses below each cover type refer to the total number of species collected in each habitat.

between the ABC undisturbed and salvaged forests. The ABC and JP wind-disturbed plots formed a cluster with approx. 90% similarity in species composition. The JP salvaged plots were the most dissimilar from the rest of the group with only 35% similarity in species composition. Cluster analysis of species composition without the numerically dominant species, *P. melanarius*, revealed that the cover type-land-area treatment combinations clustered into two distinct groups: (1) JP undisturbed, wind-disturbed, and salvaged forests; and (2) ABC undisturbed, wind-disturbed, salvaged, burned, and JP burned forests (Fig. 11). As in the analysis with *P. melanarius*, there was a 100% similarity in species composition between the ABC and JP burned forests. The undisturbed and wind-disturbed forests in both the cover types formed a cluster, whereas the JP salvaged forest was the most dissimilar from the rest of the group with only 35% similarity in species composition.

3.3.2. Baited pitfall traps

Cluster analysis of ground beetle species composition among the cover type-land-area treatment combinations revealed two distinct groups: (1) JP burned forests; and (2) ABC and JP undisturbed, wind-disturbed, and salvaged forests (Fig. 12). For baited pitfall traps, the only data collected in the ABC cover type was collected in 2000. There was 100% similarity in species composition among the ABC undisturbed and JP wind-disturbed forests, which formed a cluster with the rest of the undisturbed and wind-disturbed forest plots. The JP and ABC salvaged forests had the most dissimilar species composition with only 38% and 60% similarities, respectively. The structure of the dendrogram for the percentage similarity of species composition without *P. melanarius* remained the same as above except that there was an overall 5–10% decrease in the similarities among the cover type-land-area treatment combinations (Fig. 13).

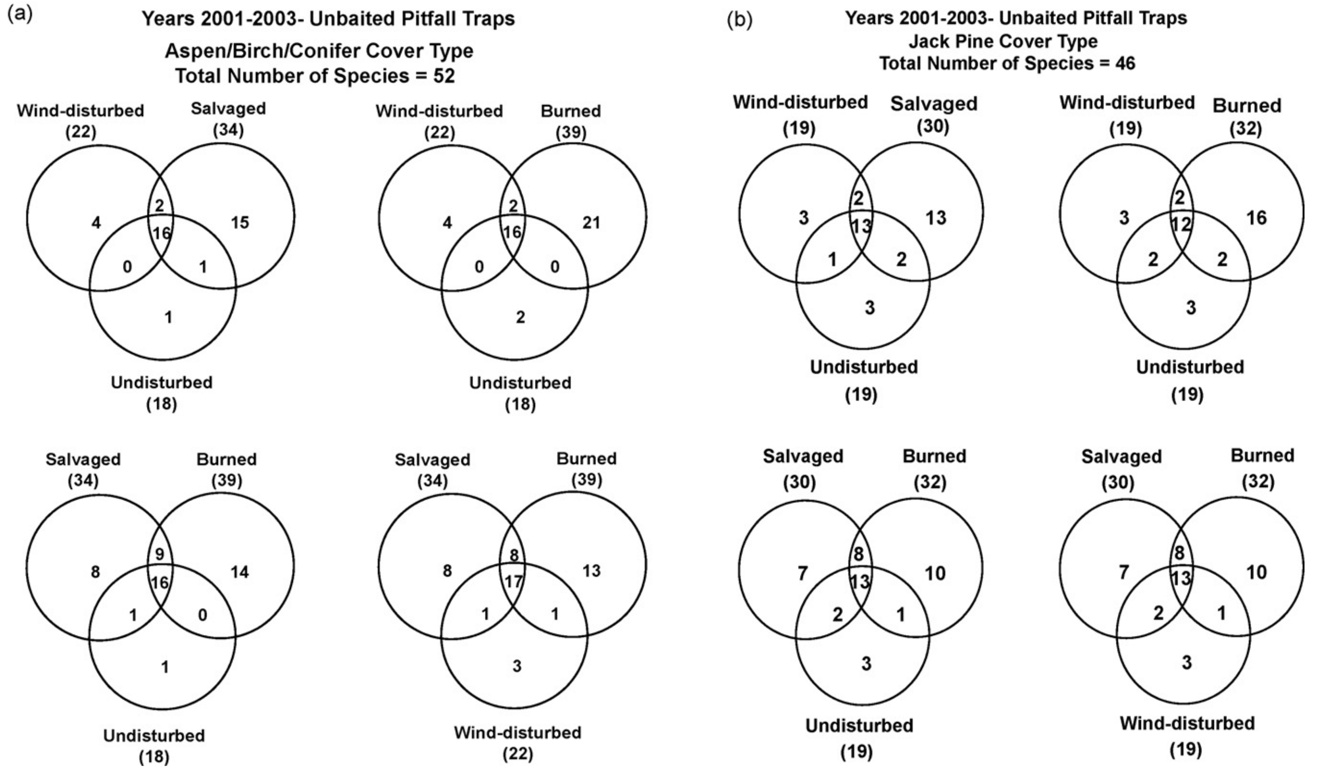

Fig. 7. Venn diagram depicting the total number of ground beetle species trapped in unbaited pitfall traps in 2001–2003, and shared by or unique to the undisturbed, wind-disturbed, salvaged, and burned plots in the aspen/birch/conifer (a) and jack pine (b) cover type. Values in parentheses refer to the total number of species collected in each habitat.

4. Discussion

4.1. Ground beetles in land-area treatments

4.1.1. Comparisons between undisturbed and wind-disturbed forests

More beetles were caught in undisturbed as compared to wind-disturbed sites (Table 3, Figs. 2–5). Saint-Germain and Mauffette (2001) also reported a decrease in ground beetle catches, especially of forest species, after a severe ice-storm in 1998 in maple stands of southwestern Quebec. However, they caught only 211 ground beetles over 2 years. Similarly, Bouget (2005) reported a decrease in ground beetle catches (especially of forest specialists) in windthrow gaps after a severe storm in 1999 in oak-hornbeam, aspen, and birch forests in France. These combined studies suggest that in the short term, populations of forest ground beetles may be adversely affected by severe windthrow.

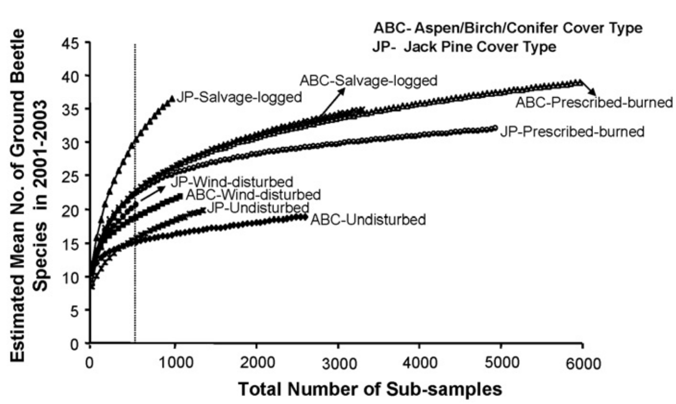

Fig. 8. Estimated mean number of ground beetle species trapped in 2001–2003 in unbaited pitfall traps in the undisturbed, wind-disturbed, salvaged, and burned land-area treatments in the two forest cover types from rarefaction analysis. Vertical line on the figure indicates the lowest sub-sample size.

Among abundantly and commonly trapped species, there were no differences in the catches of *P. adstrictus* between undisturbed and wind-disturbed sites. However, more *P. coracinus*, *P. pensylvanicus*, and *Sp. lecontei* were caught in undisturbed sites. These three species are known to be forest species preferring moist habitats in moss or leaf-litter (Lindroth, 1961–1969). Apparently, *P. adstrictus* was able to successfully find food, shelter, and overwintering sites in the post-wind-disturbed landscape, which included newly created diverse micro-habitats such as root mounds, soil pits, and fallen coarse-woody debris on the forest floor (Beatty and Stone, 1986). Major physical changes after forest openings include lowered humidity and increased temperature on the forest floor (Chen et al., 1999). In general, these changes have been reported to adversely affect ground beetle species in boreal forests (Thiele, 1977; Niemelä, 1997,1999). In support of this in our study, *P. coracinus*, *P. pensylvanicus*, and *Sp. lecontei* were trapped in lower numbers and apparently were adversely affected in the short-term

Table 8
Simpson's diversity indices for ground beetles caught in two cover types and four land-area treatments, Superior National Forest, Cook Co., Minnesota, USA

Cover type	Trap type	Undisturbed	Wind-disturbed	Salvaged	Burned
Aspen/birch/conifer	Unbaited traps	1.184	1.181	1.18	1.442
Jack pine	Unbaited traps	1.256	1.208	1.18	1.47
	Baited traps	1.197	1.17	1.25	1.551

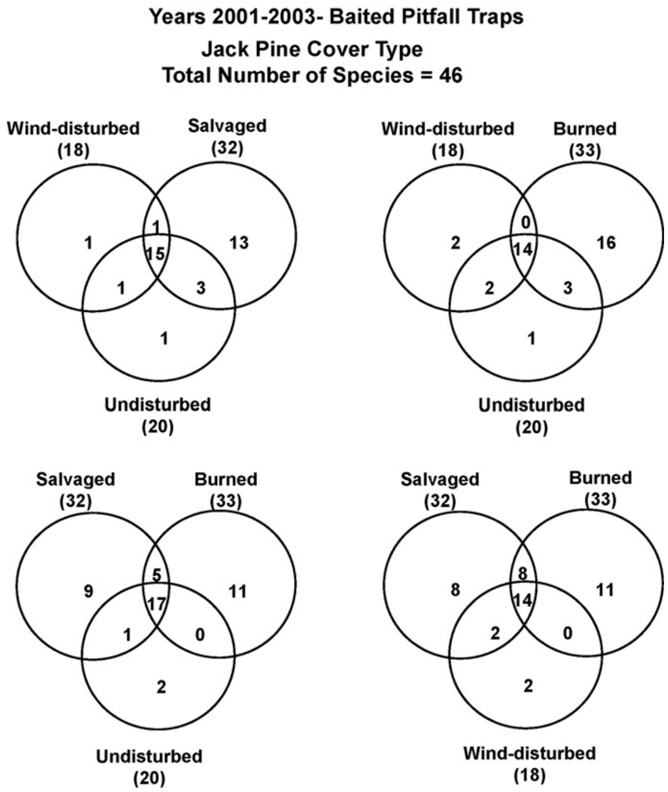

Fig. 9. Venn diagram depicting the total number of ground beetle species trapped in baited pitfall traps in 2001–2003, and shared by or unique to the undisturbed, wind-disturbed, salvaged, and burned plots in the jack pine cover type. Values in parentheses refer to the total number of species collected in each habitat.

by soil-disturbance and increases in coarse woody debris after this wind-disturbance event.

Results from unbaited pitfall traps indicated that ground beetle species composition in wind-disturbed sites in the two forest cover types was approx. 90% similar (Fig. 10). In the analysis, these wind-disturbed forests formed a cluster with the JP undisturbed sites with 75% similarity in species composition, whereas the ABC undisturbed sites formed a cluster with the ABC salvaged sites (95% similarity in species composition). It appears that the ground beetle successional trajectories in the JP undisturbed sites were similar to those in the wind-disturbed sites, whereas those in the ABC undisturbed sites were similar to those in the salvaged sites. Such trends suggest that there may have been initial differences in beetle assemblages in the undisturbed forests in the two cover types (see below), but the wind-disturbance may have removed these differences. When *P. melanarius* was removed from the cluster analysis, ground beetle species composition in undisturbed and wind-disturbed sites in both cover types became similar based on data from both unbaited (JP-70%, ABC-95%) and baited (ABC-75%, JP-90%) traps (Figs. 11 and 13). This suggests that the successional trajectories of ground beetles in the undisturbed and wind-disturbed forests may have been the same if *P. melanarius* were absent or present in low numbers in these forests.

4.1.2. Comparisons among undisturbed, wind-disturbed, salvaged, and burned forests

Overall, more ground beetles were caught in burned forests than in the rest of the land-area treatments (cf. Niwa and Peck, 2002; Saint-Germain et al., 2005), and in baited pitfall traps the numbers trapped appeared to increase during the year after the prescribed-burning. Species-level analyses indicated that this trend is partly driven by *P. melanarius*, which was the most abundant beetle in our study, and was caught in greater numbers in the JP burned sites. *P. melanarius* was introduced in the early 1900s from Europe. Since then, it has colonized the interior of the North American continent from both the Atlantic and Pacific oceanic sides (Lindroth, 1961–1969; Bousquet and Larochelle, 1993; Will et al., 1995). Gandhi et al. (2005) described the regional colonization of the North Central United States and South Central Canada by *P. melanarius*; it was recorded from southern Minnesota as early as 1990 from museum records. This beetle is associated with disturbed and open-habitats such as agricultural land and managed forest landscapes (Lindroth, 1961–1969). The aggressive landscape-level colonization by *P. melanarius* is facilitated by wing dimorphism. They are short-winged in relatively stable habitats, but long-winged in less stable or in frontier habitats (Niemelä and Spence, 1991,1999), such as those created by prescribed-burning (Roughley, 2001). Since prescribed-burning was a treatment in our

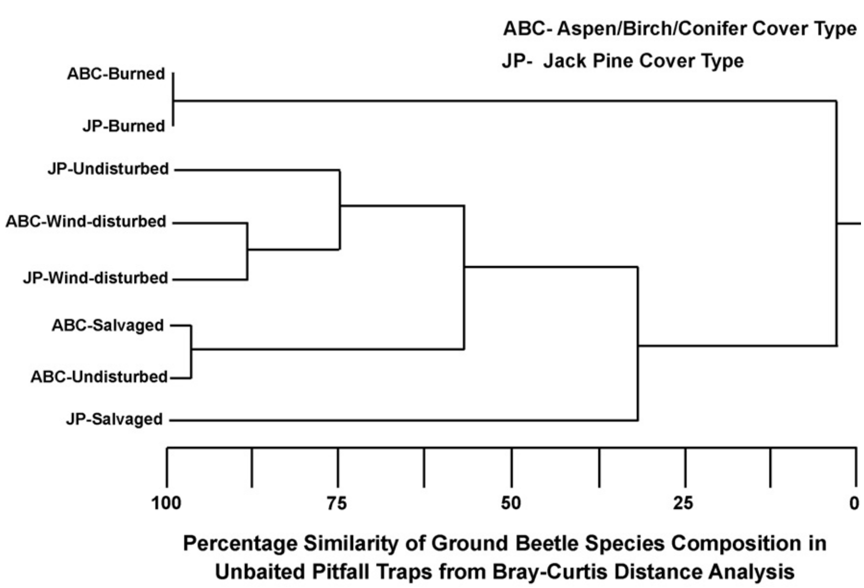

Fig. 10. Dendrogram of the percentage similarity of the ground beetle species trapped in unbaited pitfall traps in 2000–2003 in the undisturbed, wind-disturbed, salvaged, and burned plots in the aspen/birch/conifer and jack pine cover types.

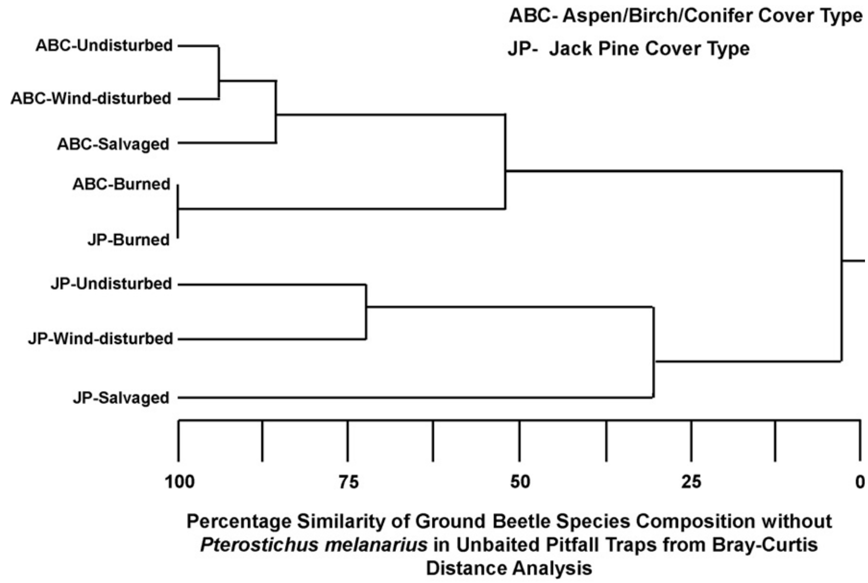

Fig. 11. Dendrogram of the percentage similarity of the ground beetle species trapped in unbaited pitfall traps in 2000–2003 in the undisturbed, wind-disturbed, salvaged, and burned plots in the aspen/birch/conifer and jack pine cover types without *P. melanarius*.

study area between the fall of 2000 and spring of 2001 (i.e., during the ground beetle overwintering period), we hypothesize that the beetles rapidly colonized the newly burned areas from the surrounding areas and established breeding populations that increased during the time-frame of our study. After fires in the tall-grass prairies in Manitoba, the populations of *P. melanarius* increased 1 year after burning, and then reverted back to their original levels from then onwards (Roughley, 2001). Unlike the results reported by Roughley (2001), in our study, the trap catches of *P. melanarius* 2 years after the burn remained high in burned sites. These results suggest that multiple disturbances such as burning after a windstorm may enhance the invasion response by exotic species like *P. melanarius*. Collins et al. (2007) assessed the initial effects of fuel-reduction strategies on understory plant communities in a Sierra Nevada mixed-conifer forest (California), and found low, but significant, increases in abundance and richness of exotic forbs subsequent to mechanical and mechanical plus fire land-area treatments. *P. melanarius* may be another example of an exotic invader that can alter forest processes and possibly influence future disturbance regimes (reviewed for other taxa in Mack and D'Antonio, 1998).

Our prescribed-burned sites were salvaged logged prior to burning, yet they appeared to establish and maintain reproductive populations of pyrophilous ground beetle species, such as *S. obsoleta* (Say) and *S. quadripunctata* (DeGeer), which were only trapped in prescribed-burned sites in both cover types. Pyrophilous species are strongly attracted to newly burned areas and apparently use the burned areas for reproduction and feeding activities (Lindroth, 1961–1969; Liebherr, 1991; Holliday, 1984; Wikars, 1992,1995; Dajoz, 1998). *S. obsoleta* was caught in 2001 and 2002, whereas *S. quadripunctata* was caught only in 2001 indicating that they were active in our plots for only 1–2 years after the fire (Dajoz, 1998; Saint-Germain et al., 2005; Boulanger and Sirois, 2007). Both *P. melanarius* and several *Harpalus* spp. (see

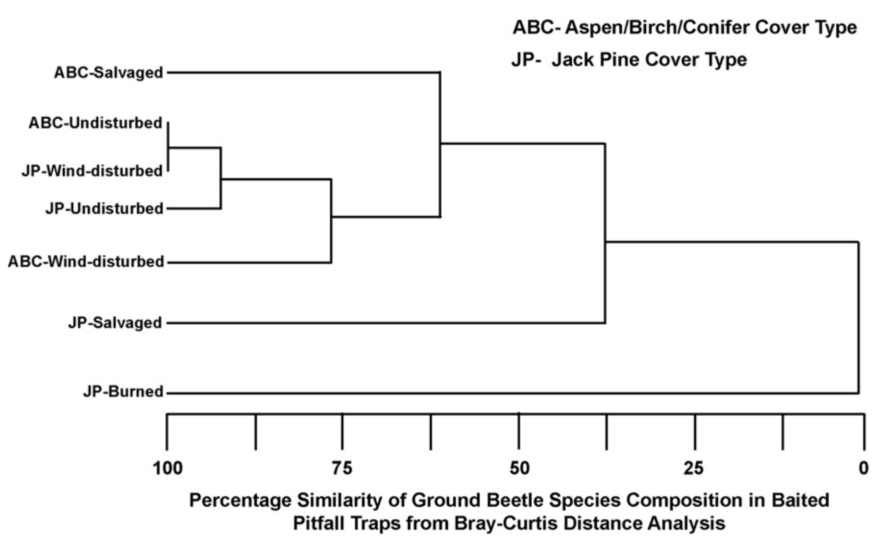

Fig. 12. Dendrogram of the percentage similarity of the ground beetle species trapped in baited pitfall traps in 2000–2003 in the undisturbed, wind-disturbed, salvaged, and burned plots in the aspen/birch/conifer and jack pine cover types.

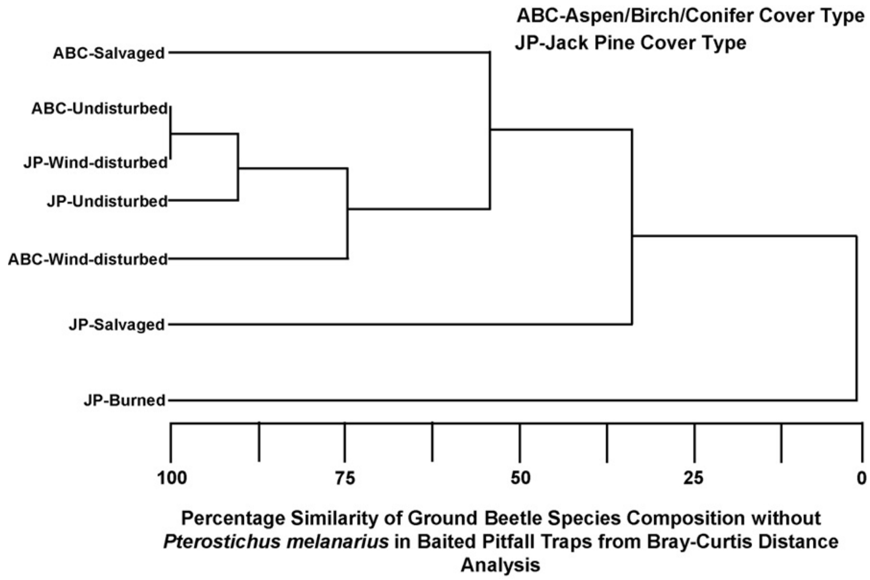

Fig. 13. Dendrogram of the percentage similarity of the ground beetle species trapped in baited pitfall traps in 2000–2003 in the undisturbed, wind-disturbed, salvaged, and burned plots in the aspen/birch/conifer and jack pine cover types without *P. melanarius*.

below) also exhibited a tendency toward pyrophilly in our study. A number of pyrophilous species are red-listed in European forests due to the efficient suppression of wildfire and the use of clear-cutting as a stand replacement practice over the past two centuries (Heliövaara and Väisänen, 1984; Wikars, 1992,1997). In contrast to the salvage-logging in our study, clear-cutting before burning of a forest prevented holarctic *S. quadripunctata* from establishing successful breeding populations in Finnish forests (Wikars, 1995). The sub-boreal forests of North America have been managed for less time than the European forests, and our data suggest that prescribed-burning, even after salvage-logging, may maintain populations of pyrophilous beetles in northeastern Minnesota. It is unknown if logged and prescribed-burned forests would sustain sizes of beetle populations similar to those of the naturally burned forests because there may be inherent differences in habitat structure that may further affect populations of pyrophilous species.

The responses of ground beetles to the land-area treatments were species-specific. For example, *P. coracinus*, *P. pensylvanicus*, and *Sp. lecontei* were caught in greater numbers in the undisturbed than in burned forest sites. In contrast, *Agonum cupripenne*, *Po. l. lucublandus*, *P. adstrictus*, and *S. impunctatus* were strongly associated with both the salvaged and the burned forest sites. In particular, the catches of *S. impunctatus* increased from 2001 to 2003 in the disturbed forests. *A. cupripenne*, *Po. l. lucublandus*, and *S. impunctatus* are species typical of disturbed, open, and dry habitats (Lindroth, 1961–1969) such as those found in the salvaged and burned forests. *Synuchus impunctatus*, in particular, has been found to be both a forest and an open-habitat species in the northeastern United States and Canada (Saint-Germain and Mauffette, 2001; Pearce et al., 2003; Moore et al., 2004). The distribution of *S. impunctatus* may be determined by the amount of coarse-woody debris (Pearce et al., 2003) and the newly available habitats present in the recently burned forests. Because females of *P. adstrictus* oviposit on logs, this species is dependent upon coarse-woody debris for the completion of its life-cycle (Goulet, 1974). Thus, we expected to find this species in greater abundance in the wind-disturbed forests. However, *P. adstrictus* was more abundant in the burned forests. Unexpected and variable responses from *P. adstrictus* and *S. impunctatus* in this study indicate that some ground beetle species may have a range of habitat associations based on the forest types and resulting local micro-habitat conditions (Rykken et al., 1997).

Comparison of the timing of the prescribed-burning with the seasonal activity patterns of the species (Gandhi, 2005) raises the possibility of immediate mortality from incineration (Saint-Germain et al., 2005). Particularly vulnerable species were *C. ingratus*, *P. adstrictus*, and *P. pensylvanicus*, which had the greatest activity in early summer, and *P. melanarius*, *Po. l. lucublandus*, and *S. impunctatus*, which had the greatest activity in late summer (Gandhi, 2005). Early and late summer beetle activity periods coincided with the intervals of the prescribed-burning (Fig. 1a). *Calathus ingratus*, *P. adstrictus*, and *P. pensylvanicus* may have been less affected because they likely overwinter as adults and could have escaped the early and late summer fires by flying. However, *P. melanarius*, *Po. l. lucublandus*, and *S. impunctatus* likely overwinter as larvae, preventing rapid dispersal and escape. Whether or not they experienced mortality from incineration, the responses of *P. coracinus*, *P. pensylvanicus*, and *Sp. lecontei* in unburned vs. burned forest plots suggests that burning negatively affected their activity-abundance.

Overall, burned and salvaged sites harbored greater total numbers of species as well as the most unique numbers of species when compared with the undisturbed and wind-disturbed sites. Open-habitat ground beetle species (e.g., species of *Amara* and *Harpalus*) rapidly colonize newly disturbed and opened areas, and establish populations in regenerating forests (Niemelä et al., 1993; Spence et al., 1996; Werner and Raffa, 2000; Fernández and Costas, 2004; Gandhi et al., 2004). These species display high dispersal ability and are known as 'super-tramp species' or 'extreme *r*-strategists' (Holliday, 1984,1991). Except for *A. coelebs*, *H. innocuus* LeConte, and *H. somnulentus* Dejean, we trapped the remaining eleven *Amara* and *Harpalus* species only in the salvaged and burned sites. Five of the *Harpalus* species were associated primarily with burned sites, confirming the results of Holliday (1991) from naturally burned boreal forests. These open-habitat species are strong competitors and are known to slowly out-compete forest species in the intensively managed European forests (Lindroth, 1972; Niemelä, 1997,1999). Due to the post-wind-disturbance management activities in the Superior National Forest (USDA Forest Service, 2000), it is likely that these managed forests would be colonized by these species.

Burned forests had the greatest species diversity, irrespective of cover type. Similar results have been found for naturally burned (Holliday, 1984, 1991; Villa-Castillo and Wagner, 2002) and prescribed-burned (Kinsella, 2003; Apigian et al., 2006a,b) forests. In contrast, in the Pacific Northwest region of North America, Niwa and Peck (2002) reported a lower abundance of ground beetles in unburned sites but similar species richness and diversity indices between burned and unburned sites. In addition to the pyrophilous and open-habitat species noted above, the young regenerating burned plots in our study were also colonized by rare species such as *Ag. cupreum* Dejean, *Ag. dilutipenne* Motschulsky, *B. quadrimaculatum oppositum* Say, *B. lugubris* (LeConte), *N. aquaticus*, and *Tachyta nana kirbyi* Casey. Most of these rarer ground beetle species (except for *Ag. dilutipenne* and *B. lugubris*) are typical of open and dry habitats (Lindroth, 1961–1969). Although ground beetles were only a fraction of the Coleoptera surveyed, Apigian et al. (2006b) reported that in the Sierra Nevada mixed-conifer forest, alterations in the beetle assemblage due to prescribed burn and mechanical treatments were driven by changes in the numbers of rare species of Coleoptera. Interpreting our results and those of others, it appears that burned forest habitats may represent temporal refugia for ground beetle species that typically occur in open and dry habitats.

In North American sub-boreal forest habitats, fuel-reduction treatments especially prescribed-burning subsequent to a severe wind-disturbance may alter successional trajectories of ground beetle assemblages. In our study, JP salvaged and ABC and JP burned sites had the most distinct ground beetle assemblages in the analysis of trap catches from both unbaited and baited pitfall traps. In these cover-type-land-area-treatment combinations only 30% of the ground beetle species were shared with the rest of the combinations. Similar results were found in Europe for insect (Duelli et al., 2002; Wermelinger et al., 2002) and in North America for vegetation responses to salvaging subsequent to wind-disturbances (Elliot et al., 2002). On several continents, successional trajectories of vegetation (Nieuwstadt et al., 2001; Purdon et al., 2004), vertebrates (Lindenmayer et al., 1999), and songbirds (Greenberg et al., 1995; Morissette et al., 2002) were altered by salvage-logging subsequent to wildfire. Although the native biota are either adapted to or recover easily from natural disturbances, multiple disturbances apparently alter the course and pattern of biotic recovery during the short interval following the disturbance(s).

Ground beetle species composition was identical in the ABC and JP burned cover types, irrespective of the presence of *P. melanarius* in the analysis. Hence, the disturbance type may influence species composition more than the nuances of cover type in this sub-boreal landscape. A possible reason for such highly similar species composition could be that *Populus tremuloides* was regenerating in high numbers in the burned areas of both cover types. This may have led to similar understory plant species composition, which in turn could lead to similar micro-habitat conditions that are known to directly influence ground beetle species composition (Thiele, 1977).

Ground beetle species composition analysis without *P. melanarius* in unbaited pitfall traps resulted in greater similarity (50%) of the burned forests with the rest of the land-area treatments. This suggests that ground beetle succession in the burned forests may have undergone similar trajectories to that of the undisturbed and wind-disturbed forests if *P. melanarius* were absent or present in low numbers in these sub-boreal forests. In addition to driving differences in ground beetle species composition between the undisturbed and wind-disturbed forests, *P. melanarius* also appeared to drive differences in species composition between the burned forests and rest of the land-area treatments in this sub-boreal landscape.

4.2. Ground beetles in ABC and JP cover types

In 2000, similar numbers of ground beetles were trapped in the aspen/birch/conifer (ABC) and jack pine (JP) cover types (in both unbaited and baited traps), suggesting that these habitats harbored similar ground beetle populations. However, during the years 2001–2003, ground beetle catches in unbaited traps were 34% greater in the ABC than in the JP cover type (except in the burned sites). In contrast to coniferous forests, deciduous forests have a well-defined litter layer where various species of mosses, forbs, and shrubs dominate the forest floor (see Supplementary data). Two to four years after the disturbance event, this deciduous forest litter layer may have provided more over-wintering habitats, shelter from predators, and perhaps greater prey availability than the needle-laden litter layer in the JP forest, thus contributing to the relatively higher trap catches of ground beetles.

Species-level analyses also revealed that *Ag. retractum*, *C. ingratus*, *Pl. decentis*, *P. adstrictus*, and *Sp. lecontei* were trapped more frequently in the ABC than in the JP cover type (Tables 3 and 5). In northwestern Ontario, similar results were reported for *Ag. retractum*, *C. ingratus*, and *Pl. decentis* where they were more associated with aspen than with black spruce and mixedwood forests (Pearce et al., 2003). Similarly, in northwestern Alberta, *Pl. decentis* was more associated with deciduous-dominated than coniferous-dominated stands (Work et al., 2004). Hence, the ground beetle species noted above and particularly *Pl. decentis*, appear to be adapted to aspen-dominated forests.

Ground beetle species richness and diversity were quite similar in the ABC and JP cover types. Because of the greater amount and complexity of litter-fall generally present in deciduous forests, we had expected the ABC cover type to have greater ground beetle species richness and diversity than the JP cover type. Similar results were reported by Pearce et al. (2003) where estimated ground beetle species diversity was similar in the aspen- and spruce-dominated sub-boreal forests in Ontario. It appears that although larger populations of ground beetles were present in the ABC cover type, both cover types harbored similar numbers of ground beetle species.

Unbaited and baited pitfall trapping revealed that the ABC and JP cover types contained 29 ground beetle species that were uniquely present in one or the other type (Table 3). Unbaited trapping revealed 24 of the unique species (Fig. 6). Most of these species were quite rare (represented by a single or a few individuals), and therefore, they could be transients in either of the forest cover types. However, *Sp. n. brevoorti* and *Myas cyanescens* Dejean were caught in sufficient numbers (>100 individuals) to indicate that these species were exclusively associated with the ABC and JP cover types, respectively. *Sphaeroderus n. brevoorti*, reported for the first time in Minnesota from our study (Gandhi et al., 2005), is known to be a forest species preferring moist habitats in leaf litter, whereas *M. cyanescens* is known to prefer dry and sandy soils (Lindroth, 1961–1969; Pearce et al., 2003). Anticipated decline of the JP cover type in the Superior National Forest due to the efficient suppression of wildfires (Heinselman, 1973) and mortality by bark beetles and woodborers (Gandhi, 2005) may increase the risk of local extinction of ground beetle species such as *M. cyanescens*. On the other hand, due to an increase in the area of the ABC cover type after the last logging-era of the early 1900s and a concurrent decrease in the pine stands (Heinselman, 1973; Frelich and Reich, 1995), populations of species such as *S. n. brevoorti* may likely be well-maintained.

Cluster analysis of ground beetle composition from unbaited pitfall traps did not group the species by land-area treatments based on cover types. However, cluster analysis of unbaited pitfall trap data without the invasive and dominant *P. melanarius* revealed that with the exception of the burned sites, the beetle assemblages in the two cover types were only 5% similar, i.e., the compositions in the various land-area treatments were clustered primarily based on cover type (Fig. 11). *P. melanarius* appears to be a generalist in terms of cover type, and it can be perhaps viewed as a major 'homogenizing' or 'diluting' factor in this sub-boreal forest at the landscape-level. Ground beetle species composition differences driven by cover type were not evident after the removal of *P. melanarius* from the analysis of data from baited pitfall traps (Fig. 13).

4.3. Ground beetles and baited pitfall traps

Ground beetles did not respond to baits used for the baited pitfall traps. It is unclear how the use of pinenes and ethanol baits affects individual ground beetle species as there have been no comparable studies. There have been studies on the effects of formalin, water, detergent, glycerol, ethylene glycol, and propylene glycol as killing agents in the traps on the catching efficiency of ground beetles (Luff, 1968; Greenslade and Greenslade, 1971; Holopainen, 1992; Weeks and McIntyre, 1997; Pekár, 2002). These studies found that ethylene glycol, propylene glycol, and formalin generally increase trap catches relative to water alone. We did not find similar trends in our study by using pinenes and ethanol as baits for the traps.

5. Conclusion

Our study indicates that ground beetles can be used effectively as bioindicator taxa to assess short-term changes in forest stands after major disturbances. We documented a species-rich assemblage of ground beetles inhabiting the sub-boreal forests of northeastern Minnesota, and recorded 13 ground beetle species not previously reported from Minnesota. More ground beetles were trapped in the aspen/birch/conifer (ABC) than in the jack pine (JP) cover types, and there were differences in species composition between the two cover types. For example, 29 rare species were caught only in one or the other cover type (Table 3) and two common species, *Sp. n. brevoorti* and *M. cyanscens*, were caught only in the ABC and JP types, respectively. However, species richness and diversity were both similar in the cover types. In this region of the U.S., large-scale conversion from JP to ABC cover type may be problematic for ground beetle species that are adapted to micro-habitats characteristic of the conifer-dominated forests.

There were also differences in ground beetle trap catches and composition among the undisturbed/wind-disturbed forests and the two fuel-reduction treatments (salvage-logged and prescribed-burned). Surprisingly, in the short-term, the catastrophic wind-disturbance event seemed to adversely affect populations of certain forest species such as *P. coracinus*, *P. pensylvanicus*, and *Sp. lecontei*, which were generally caught more frequently in undisturbed sites than in any other land-area treatment sites. The greatest number of ground beetles were caught in the burned forests. A number of species such as *Ag. cupripenne*, *Po. l. lucublandus*, *P. adstrictus*, *P. melanarius*, and *S. impunctatus* were caught more frequently in salvaged and burned sites, sometimes depending upon the cover type and year. Greater numbers and the most unique ground beetle species, especially open-habitat and pyrophilous species, were trapped in the burned sites. The most unique species composition was also recorded in the burned and JP salvaged sites. This suggests that although salvaging and burning treatments were staggered in terms of timing, both of them have the potential to change the faunal attributes of wind-disturbed forests.

P. melanarius, an introduced species from Europe, was the most numerically dominant (10,523 adults) ground beetle species in this forest in 2000–2003. This species was trapped in both cover types and in all land-area treatments, but it was exceptionally abundant in prescribed-burned sites. Removal of *P. melanarius* from the species composition analysis changed the clustering patterns towards greater similarity in the ground beetle species composition between the ABC and JP forests, between undisturbed and wind-disturbed forests, and among burned forests and the rest of the land-area treatments. In addition, similarities in species composition between salvaged and burned sites decreased in the baited pitfall traps. Such trends indicate that (1) *P. melanarius* is a cover type generalist; and (2) the numerical abundance of *P. melanarius* in the disturbed areas has the potential to alter ground beetle successional pathways.

At present, we cannot assess either the isolated effects of prescribed-burning only or the effects of burning conducted a year later than salvaging on ground beetle assemblages in these sub-boreal forests. It is likely that changes in ground beetle attributes and especially the response of *P. melanarius* to burned forests are because of the combinations of three disturbances i.e., windthrow, salvaging, and prescribed-burning in the same stands and/or because of delayed burning. For example, in prairie habitats in southwestern Alberta, sites that were prescribed-burned without logging had higher ground beetle species richness and diversity than sites that were burned with logging (Kinsella, 2003). Although burning alone was associated with more change in assemblage structure and higher species richness of all Coleoptera in a Sierra Nevada mixed-conifer forest, the combination of burning and mechanical treatment resulted in a slightly different community-level response than from the fire treatment alone (Apigian et al., 2006b).

Our study has implications for landscape-level research on ground beetles in future disturbance ecology studies. The ground beetle species monitored here showed immediate responses to altered structural and compositional attributes of forests from fuel-reduction treatments. However, we did not observe major shifts in trap catches, and species richness, diversity, and composition within the 3-year period after the disturbances. It may take much longer for faunal turnover within the habitats, which would necessitate sampling these sites every 10 years to assess long-term changes in faunal successional pathways. Sampling during these return intervals may also capture the impact of other landscape-level disturbances such as wildfires (USDA Forest Service, 2007), leading to the potential for even more complex and richer ecological interactions.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2008.06.011.

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