Effects of a recent wildfire and clearcuts on ground-dwelling boreal forest spider assemblages

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Abstract: Ground-dwelling spider (Araneae) assemblages were compared between recent clearcuts and burned black spruce (*Picea mariana* (Mill.) BSP) forests. Spiders were sampled using pitfall traps placed in 6 recently burned sites, 6 recently clear-cut sites, and 6 undisturbed sites in eastern Quebec, Canada. A total of 2935 individuals from 95 spider species were identified. Catch rates for hunting spiders were significantly higher in the clear-cut stands than in the burned stands, but between-stand species turnover of hunting spiders was twice as high in the burned stands as in the clear-cut stands. Web-building spiders had similar catch rates in the three stand types, but had the highest species turnover and gamma diversity in the undisturbed sites. Correspondence analysis showed that the composition of the spider assemblages varied among the three types of stands. Spider assemblages found in clearcuts were associated with environmental variables reflecting dry, open, disturbed forest floor, while assemblages found in burned stands were correlated with high percentages of shrub cover and dried moss–lichen substrate and deeper litter. We conclude that ground-living spider assemblages in boreal forest respond very differently to clearcuts and fires and we suggest modifications to present forestry practices to create disturbances that are more similar to wildfires.

Résumé : Nous comparons la réaction des assemblages d'araignées (Araneae) qui vivent au sol à la suite de perturbations récentes dans la pessière noire (*Picea mariana* (Mill.) BSP). Les araignées ont été récoltées à l'aide de pièges-fosses dans six sites récemment coupés à blanc, six sites récemment brûlés et six sites non perturbés dans l'est du Québec, au Canada. Au total, 2935 individus représentant 95 espèces d'araignées ont été identifiés. Le taux de capture des araignées chasseresses était significativement plus élevé dans les peuplements coupés à blanc que dans les peuplements brûlés leur diversité bêta était deux fois plus élevée dans les sites brûlés que dans les sites coupés à blanc. Les araignées qui tissent des toiles avaient des taux de capture similaires dans les trois types de peuplements mais leur renouvellement en espèces et leur diversité gamma étaient les plus élevés dans les sites non perturbés. Une analyse de correspondance montre que la composition des assemblages d'araignées est caractéristique de chacun des traitements. Les assemblages d'araignées récoltées dans les sites coupés à blanc sont associés aux milieux secs et ouverts dont le sol est perturbé. Les assemblages d'araignées récoltées dans les sites brûlés sont associés à un pourcentage élevé de couvert arbustif, à un substrat composé de mousses et de lichens séchés et à une épaisse litière. Nous concluons que les assemblages d'araignées qui vivent au sol en forêt boréale réagissent très différemment à la coupe à blanc et aux incendies de forêt et nous suggérons des modifications aux pratiques forestières visant à créer des perturbations plus similaires à celles qui sont causées par les incendies de forêt.

Introduction

Over the last decade, research on sustainable management of the boreal forest has been aimed towards developing forest-harvesting practices that are based on our understanding of patterns and processes that occur under natural disturbance regimes (Anglestam 1998; Simberloff 2001; Bergeron et al. 2002). The strategy is to conduct logging in such a way that the disturbance pattern created on the landscape mimics the spatial and temporal disturbance pattern created by natural disturbances such as wildfire (Hunter 1993). The organisms associated with the boreal forest have evolved in the presence of natural disturbances over long time periods (Ontario Ministry of Natural Resources 2001; Bergeron et al. 2002), and it is therefore assumed that they are pre-adapted to management regimes that mimic landscape patterns and processes occurring with natural disturbances, and that they will persist under such management regimes. A first step towards developing such new sustainable forest-management approaches is to evaluate the main differences between the ef-

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fects of current logging practices and natural disturbances on the flora and fauna (Nguyen-Xuan et al. 2000).

Since the early 1980s several comparative studies have examined the effects of wildfires and clearcuts on various aspects of boreal-forest ecosystems. Differences in the effects of the two types of disturbance were found in studies on topics ranging from asymbiotic nitrogen fixation (Wei and Kimmins 1998) to understory plants and shrubs (Johnston and Elliott 1996; Nguyen-Xuan et al. 2000), lake water quality (Carignan et al. 2000), and bird communities (Hobson and Schieck 1999; Imbeau et al. 1999; Drapeau et al. 2002) and ground beetles (Saint-Germain et al. 2005). In contrast, small mammal abundances were not affected differently by clearcuts and wildfires (Simon et al. 2002). In Finland, Huhta (1971) compared the effects of various harvesting approaches on spiders, including the use of prescribed burning after harvest. This work offered valuable information on the responses of spider assemblages following harvesting and prescribed burning. Only one comparative study looked at the effects of wildfire and harvesting on arthropods. In mixedwood forests of the boreal plain in Alberta, Buddle et al. (2000) investigated spider assemblages in harvested and burned forests each represented by 3 age-classes (1–2, 14–15, and 28–29 years after disturbance). Their results showed that web-building spiders associated with mature forests either survived or recolonized recently cut stands faster than burned stands. They also showed that spider assemblages in burned stands had a more even species distribution early in succession, and contained several species that were found only in the burned stands.

Spiders (Araneae) are particularly well suited for comparing the effects of clearcuts and wildfire at the ground level. They are generally found in high abundance (Huhta 1971; Coyle 1981; Jennings et al. 1988; Coddington et al. 1996; Buddle et al. 2000), and individual species distributions and abundances are tightly linked to the structural attributes of the habitat (Uetz 1979, 1991; Hatley and Macmahon 1980; Pajunen et al. 1995). They are also key elements of the detritus-based and grazing food webs in forest ecosystems (Wise 1993; Atlegrim and Sjoberg 1995; Nyffeler 2000), and are known to be involved in nutrient recycling and fixation in the early stages of succession in disturbed habitats (Hodkinson et al. 2001).

The objective of the present study was to investigate the response of ground-dwelling spider assemblages to fire and logging in coniferous stands dominated by black spruce (*Picea mariana* (Mill.) BSP) in the boreal forest of Quebec, Canada. We hypothesized that wildfires and clear-cutting affect the structure of the forest floor in different ways, resulting in the occurrence of different spider assemblages. We expected that unburned patches of ground that survived a wildfire, and the varying severity of burning across the landscape, would enhance the structural complexity of the forest floor after a wildfire, leading to a more variable species composition of spider assemblages than in the harvested sites. Our goal is to provide new and more in-depth correlative information concerning the response of spider assemblages to both types of perturbation and investigate how this response is associated with the forest-floor structure left by each type of disturbance at the assemblage and species levels. Unlike past work (e.g., Huhta 1971; Buddle et al. 2000), our research focused on careful assessment of the short-term responses of spiders

to these disturbances, and our study represents the first of its kind in the black spruce boreal region of eastern North America.

Methods

Study area

The study was conducted during the summer of 2001 in Grands-Jardins Provincial Park (47°41′N, 70°41′W) and in the Réserve faunique des Laurentides (hereinafter referred to as the park and the reserve, respectively), both located in the Charlevoix region 150 km northeast of Québec (Fig. 1). For both the park and the reserve, black spruce is the dominant tree species and balsam fir (*Abies balsamea* (L.) Mill.) is codominant. The shrub layer is dominated by *Ledum groenlandicum* Retzius, *Salix* sp., *Vaccinium angustifolium* Ait., *Vaccinium vitis-idea* L., and *Kalmia angustifolia* L. The forest floor is dominated by sphagnum mosses, and *Cladonia* sp. is also common. In the late spring of 1999, a 5197-ha area of the park burned in wildfires. During the same period several sites in the reserve were clear-cut using the "cut with protection of the regeneration and of soils" (CPRS) approach.

Spider sampling

In the spring of 2001, 6 burned sites in the park, 6 clear-cut sites in the reserve, and 6 undisturbed sites in the park and the reserve were selected, for a total of 18 sites (Fig. 1). All sites selected for the study lie well within the same forest ecosystem type, and the minimal distance between sites (1 km) is more than sufficient to assure independence of our sampling sites when the home-range dispersal (<25 m²) (Cady 1984; Buddle and Rypstra 2003) of the organisms targeted in this study is considered. In each of these sites, a square 400-m² area a minimal distance of 100 m from the edges of disturbances or 100 m inside the undisturbed areas was systematically delimited by always setting the pitfall traps at the opposite corners of the 400-m² area at the extremity of the trap line. Within the 400-m² area, three 10 cm diameter pitfall traps 10 m apart were inserted in the ground with the lip or top of the trap flush with the ground. Each trap was composed of two plastic cups one within the other to facilitate the removal of the trap (inner cup) from the forest floor and minimize damage to the soil surrounding the trap during sampling. Into each trap we poured 100 mL of a 50% ethylene glycol solution. A square 10 cm × 10 cm plastic roof supported by nails in its corners was placed 5 cm above the traps. The traps were active for 6 weeks from 6 June to 17 July 2001. Since our sampling period covered the first peak in activity for most boreal-forest spider families (Aitchison-Bennell 1994; Niemela et al. 1994; Buddle 2000; Buddle and Draney 2004), we feel comfortable that it renders a good and necessary portrait of the structure of ground-dwelling spider assemblages found in our study sites that is sufficient to allow us to draw valuable inferences on the spider community's response to wildfire and harvesting. Our focus is not on the effect of the two types of disturbance on total spider richness in the systems, but rather on the response of the assemblages to the forest-floor structure left by both types of perturbation.

Fig. 1. Locations of the sampling sites in Grands-Jardins Provincial Park and the Réserve faunique des Laurentides in Quebec, Canada.
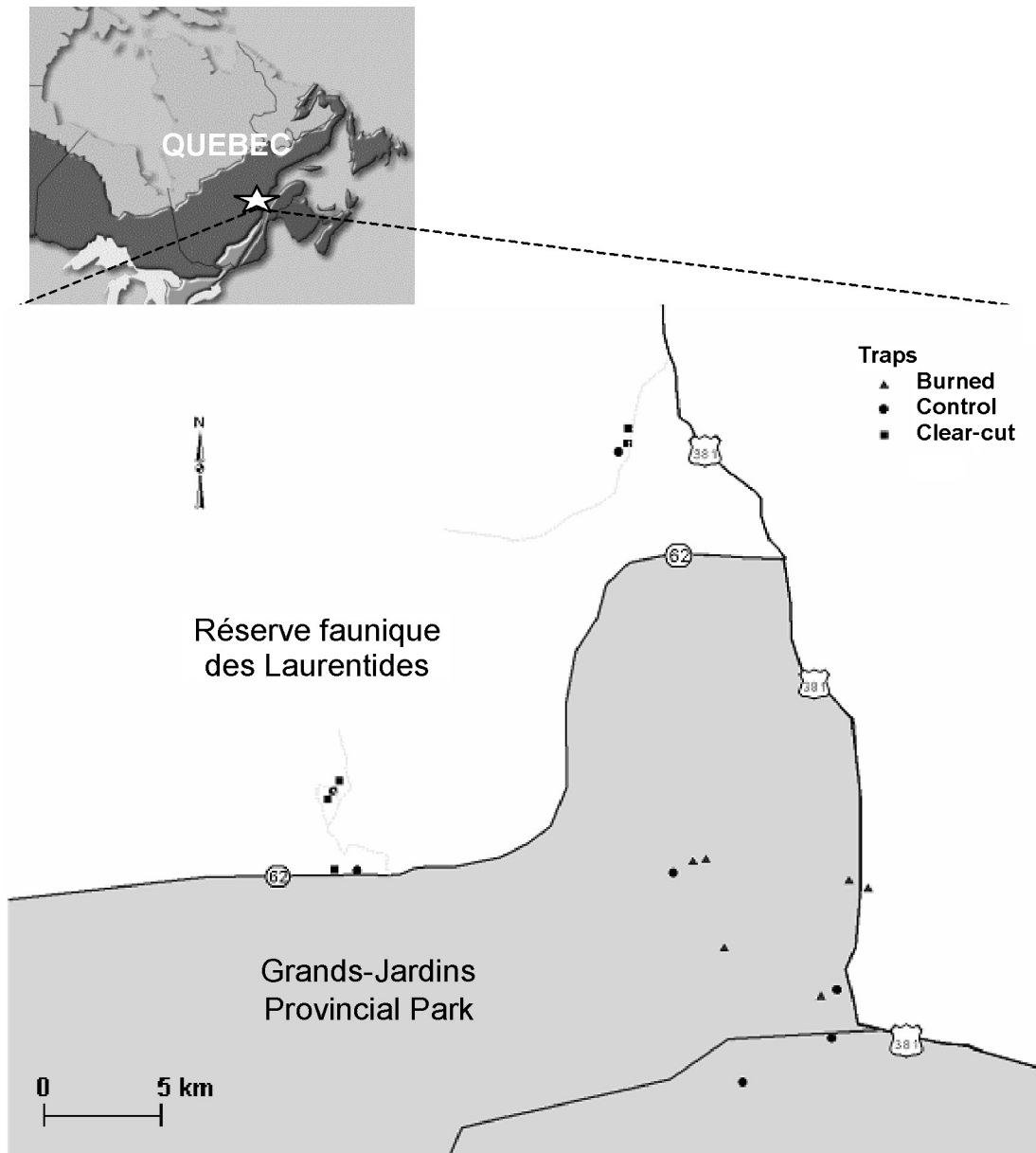
All spiders were identified to species (Dondale and Redner 1978; Dondale and Redner 1982; Dondale and Redner 1990; Platnick and Dondale 1992; Pierre Paquin, personal communication) and compared with specimens from the National Collection at Agriculture and Agri-Food Canada in Ottawa. Classification followed Platnick's (2004) *World Spider Catalog*. Vouchers of each species have been deposited in the Insectarium René-Martineau at the Centre de Foresterie des Laurentides in Québec City and also in the Canadian National Collection for species representing new records for the Province of Quebec.

Habitat structure

Five 1-m² quadrats were systematically laid out within each 400-m² site. In each quadrat we measured percent cover at ground level of moss–lichen substrate, bare soil, leaves (including needles), shrubs, and coarse woody debris (CWD).

We also measured litter depth and tree-canopy cover. Canopy cover corresponded to the canopy created by the mature dominant trees at each site and was measured following the procedure of James and Shugart (1970), except that measurements (whether canopy was present or absent) with the site tube were taken every 1 m for a total of 10 m in each cardinal direction. These values were then converted to percent canopy cover. Species-richness inventories of all vascular plants were completed, and the snags, stumps, and fallen trees in each 400-m² area were counted. We also calculated a forest floor heterogeneity index for each site as follows: we first calculated the coefficient of variation across the five plots within the site for each plot-scale environmental variable. The heterogeneity index for each site was then taken as the average of these coefficients of variation. Sites that were more heterogeneous at the local scale had larger values of the heterogeneity index. We also measured between-site het-

erogeneity within each disturbance category by calculating the coefficient of variation among sites of a disturbance category for all environmental variables and then calculated the average of these coefficients of variation.

Statistical analyses

To account for traps damaged mostly as a result of mammal predation during the sampling period, the abundance and richness values used in the analyses were converted to spider catch per trap per week. Catches from all three traps laid out at each site were pooled, as all the analyses in our study were performed at the site level. To provide a measure of species diversity robust to our sample sizes that varied between treatments, we produced rarefaction curves with the software Biodiversity Pro, Version 2 (McAleece et al. 1997).

We calculated alpha, beta, and gamma diversity of the spider assemblages. For alpha diversity, we used the estimated number of species found at each site obtained through rarefaction curves; beta diversity was the species turnover between sites within a treatment (burned, clear-cut, or undisturbed) and gamma diversity was the overall spider richness found at the treatment level. Beta diversity was estimated following Drapeau et al. (2000) by calculating the gradient length occupied by the sites of a disturbance type on the first axis of a detrended correspondence analysis.

We performed one-way ANOVAs to compare the environmental characteristics of the three treatments, burned, clearcut, and undisturbed. Spider catch rates (number of individuals per trap per week) were also compared between treatments using one-way ANOVAs. We conducted a correspondence analysis (CA) (Jongman et al. 1995; Legendre and Legendre 1998) to assess the variation in species composition of spider assemblages within and between the three treatments. The choice of CA for our ordinations resides in the fact that our undisturbed and disturbed sites provide a large enough environmental gradient, offering high chances of covering the species' low and optimal frequencies. The data structure for spider assemblages was then related to the environmental variables measured using a canonical correspondence analysis (CCA) (ter Braak 1986; Legendre and Legendre 1998; McGarigal et al. 2000) using CANOCO 4.0 for Windows© (ter Braak and Smilauer 1998). For the CCA, the environmental variables measured at the plot scale were averaged to obtain a value for each site. These included percent cover of leaves, mosses and lichens, bare soil, and CWD on the forest floor, as well as percent cover of the shrub layer and the tree canopy. Variables measured at the site level — numbers of stumps, treefalls, and snags and our calculated heterogeneity index — were also included in the CCA. All the values obtained for the environmental variables were standardized. The spider matrix used for the CCA was composed of all the species represented by more than one individual.

We also performed a CCA for the 10 most common species in each of the two spider feeding guilds, hunters and webbuilders. These two guilds are often studied separately because they respond to different environmental variables (Huhta 1971; Uetz 1975; Pajunen et al. 1995; Collins et al. 1996; Buddle et al. 2000). The hunter guild (families Agelenidae, Amaurobiidae, Clubionidae, Gnaphosidae, Lycosidae, Philodromidae, Salticidae, Thomisidae) catch their prey by means of active pursuit or use a sit-and-wait ambush tech-

nique, and are generally associated with open, well-lit habitats that have a more variable microclimate. The web-builders (families Araneidae, Dictynidae, Hahniidae, Linyphiidae (subfamilies Linyphiinae and Erigoninae), Tetragnathidae, Theridiidae) use webs to catch their prey and are associated with moist, mature closed-canopy forest containing a deep moss or lichen layer on the ground, especially in boreal ecosystems.

Results

Overall, 2935 individual spiders were collected, of which 2655 were mature adults. They belonged to 93 species from 13 families and 59 genera. Hunting spiders were numerically dominant (2336 individuals), while web-builders were represented by 599 individuals. Linyphiidae was the most diverse family, represented by 50 species, but accounted for only 16.3% of all adult spiders. The family represented by the second largest number of species was the wolf spider family (Lycosidae), with 15 species. Lycosids were the most commonly collected family, with 2054 individuals (77% of the total). The six species in the lycosid genus *Pardosa* that were found accounted for 72% of the total abundance. Thirty-two species of spiders were represented by only one individual.

Forest-floor structure and heterogeneity

There were significant differences among disturbance categories in the structure and composition of the ground surface (Table 1). At the stand level, the forest floor heterogeneity index was significantly higher in the clearcuts than in the burned sites. However, between-stand heterogeneity was higher (0.72) for burned stands than for clear-cut stands (0.42). Percent cover of the shrub layer was significantly higher in the burned sites than in the clear-cut sites (Table 1). Percent cover of mosses and lichens and litter depth were significantly higher, while the amount of CWD (mainly logging residues) was significantly lower in the undisturbed and burned sites than in the clear-cut sites. Finally, percent canopy cover and depth of the moss–lichen substrate were significantly higher in the undisturbed sites than in the clearcut and burned sites (Table 1).

Catch rates and diversity

Rarefaction curves show that the observed species richness in clear-cut and burned sites has begun to level off, while the the curve for undisturbed sites is still steep (with the exception of the estimated richness of web-building spiders at 146 individuals collected; Fig. 2C), even steeper than the other two curves at 371 individuals collected, which indicates a more diverse assemblage (Fig. 2).

There was a significant treatment effect on the total spider catch rate ($F_{[2,15]} = 18.23$, $p < 0.0001$) and on the hunting spider catch rate ($F_{[2,15]} = 26.48$, $p < 0.0001$), which were higher in clear-cut sites than in burned and undisturbed sites and higher in burned sites than in undisturbed sites (Fig. 3). There was no treatment effect on the catch rate for webbuilding spiders (Fig. 3).

There was a significant difference in total spider alpha diversity among treatments, ($F_{[2,15]} = 9.81$, $p < 0.002$), with undisturbed sites having a significantly higher diversity than burned and clear-cut sites (Table 2). At the guild level, alpha

Table 1. Environmental variables measured at undisturbed, burned (wildfire), and clear-cut sites in the black spruce boreal forest of Quebec.

Environmental variable	Undisturbed sites	Burned sites	Clear-cut sites	p value
Moss depth (cm)	5.9 ± 1.6b	0 ± 0a	0.2 ± 0.2a	<0.0001
Litter depth, A + O layers (cm)	10.0 ± 1.4a	13.8 ± 0.5a	8.9 ± 1.0b	0.01
Soil (% cover/m^2)	3.2 ± 1.2	14.8 ± 7.0	14.7 ± 4.26	ns
Leaves (% cover/m^2)	8.1 ± 1.3	10.2 ± 3.2	13.8 ± 2.7	ns
Mosses and lichens (% cover/m^2)	75.8 ± 3.0a	57.7 ± 9.8a	21.2 ± 5.5b	<0.0001
Coarse woody debris (% cover/m^2)	11.2 ± 2.0a	13.5 ± 4.0a	50.5 ± 4.2b	<0.0001
Shrubs (% cover/m^2)	30.0 ± 10.0ab	39.8 ± 4.1a	9.3 ± 3.7b	0.016
Tree canopy (% cover/m^2)	55.8 ± 9.3a	13.3 ± 3.7b	0 ± 0b	<0.0001
Within-stand heterogeneity index	0.53 ± 0.10ab	0.41 ± 0.15a	0.68 ± 0.18b	0.021
Between-stand heterogeneity index	0.58	0.72	0.42	
Plant richness (m^2)	7.2 ± 0.9	4.2 ± 0.9	6.3 ± 1.0	ns
Snags (no./400 m^2)	6.7 ± 3.7	2.3 ± 1.0	1.7 ± 0.6	ns
Stumps (no./400 m^2)	9.5 ± 3.2	24.2 ± 17.4	41.2 ± 2.9	ns
Treefall (no./400 m^2)	23.2 ± 6.9	31.8 ± 11.8	49.3 ± 3.5	ns

Note: Values are means ± SE (n = 6) from one-way ANOVAs (df = 2, 15) of the forest-floor environmental variables measured in all sites of the different treatments. Values followed by a different letter are significantly different between treatments, based on post hoc Scheffé tests (ns, not significant).

diversity of the hunting and web-builder guilds did not vary significantly among sites (Table 2). Species turnover among sites (beta diversity) was highest in the undisturbed sites for all spiders combined and for both feeding guilds (Table 2). Gamma diversity (total species richness) was highest in clearcuts for hunters and all spiders combined and highest in undisturbed sites for web-builders (Table 2).

In the hunter guild, 8 of the 10 most abundant species were lycosids, and 7 of them responded significantly to treatment (Table 3). Of these, 5 were species of the genus *Pardosa*; *Pardosa hyperborea* (Thorell) was significantly more abundant in the burned sites, while *Pardosa moesta* Banks and *Pardosa uintana* (Gertsch) were significantly more abundant in the clear-cut sites. *Pardosa mackenziana* (Keyserling) and *Pardosa xerampelina* (Keyserling) were significantly more abundant in the disturbed sites than in the control sites, while *Trochosa terricola* Thorell was significantly more abundant in the undisturbed and clear-cut sites. Of the web-builders, 4 species showed a significant response to the type of disturbance (Table 3). *Pocadicnemis americana* Millidge (Erigoninae) was significantly more abundant in the undisturbed and burned sites, while *Cryphoeca montana* Emerton (Hahniidae) was significantly more abundant in the clear-cut sites and *Sisicottus montanus* (Emerton) (Erigoninae) was significantly more abundant in the undisturbed and clear-cut sites. The web-building spider *Walckenaeria minuta* Emerton was found only in burned sites. Clearcuts had 12 species (with 2–9 individuals each) that were not found in burned stands, while 8 species found in burned stands were not found in clearcuts.

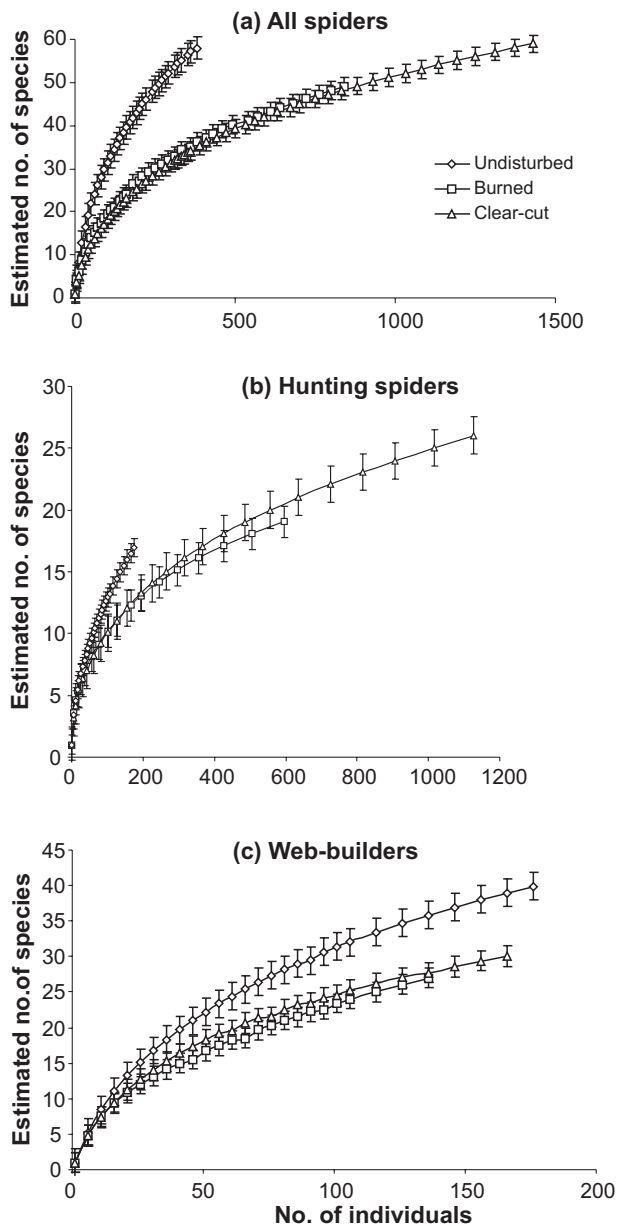## Effect of disturbances on spider assemblage composition

Over 40% of the variation in species composition was explained by the first two axes of the CA, with the four axes having a cumulative percentage of variance of 63.3% (Table 4). The spider assemblages associated with each disturbance category are clustered together in different parts of the ordination diagram. Since the distribution of the sites representing each disturbance category in the CA is similar to the distribution of the sites in the CCA (Fig. 4), we elected to not represent the CA graphically.

The CCA (Fig. 4) shows which environmental variables were most associated with spider assemblages from each treatment. The first canonical axis from the CCA explained 25.7% of the variance between the spider assemblages and the environmental variables (Table 4). It portrays a gradient from dry, open, disturbed habitats (percent cover of CWD, bare soil, and dead leaves) on the left side of the axis to closed, moist, mature, undisturbed habitat (high percent cover of mosses and lichens on the forest floor, litter depth, number of snags, and canopy cover) on the right side of the axis. The second canonical axis, explaining 19.2% of the variance, represents mainly a gradient of cover dominance from trees to shrubs (Fig. 4). The environmental variables influencing the spider assemblages in clear-cut sites were percent CWD, percent bare soil, and clearcut artifacts like the number of fallen trees and stumps. In the wildfire sites, the environmental variables most associated with spider species composition were percent cover of the shrub layer and of burned litter (Fig. 4). The spider assemblages in the undisturbed sites were mainly associated with mature stand attributes such as percent canopy cover and depth and percent cover of mosses and lichens. In Fig. 4 the spider assemblages in the undisturbed sites are much farther apart than the assemblages in either of the two disturbance categories, indicating possible greater habitat heterogeneity.

The effects of environmental variables on abundances of the 10 most abundant species of each guild are shown in Fig. 5. As the sites in Fig. 5 are distributed similarly to those in Fig. 4, they are omitted from the figure for better comprehension. The scores for the most numerous spiders of the web-building guild (circles in Fig. 5) were correlated with high percent canopy cover, depth and percent cover of mosses and lichens, and percent shrub-layer cover. Hunters (triangles in Fig. 5) are mainly located in the lower part of the second CCA axis. The ordination shows that openness of the area and percent exposed bare soil, CWD, and leaves on the ground were the factors that had the largest influence on the

Fig. 2. Rarefaction estimates of expected species richness (mean ± SE) for spiders collected in pitfall traps placed in undisturbed, burned (wildfire), and clear-cut stands: (A) All spider species, (B) hunting spiders, and (C) web-building spiders.

Fig. 3. Catch rates of spiders obtained from pitfall traps placed in undisturbed, burned, and clear-cut lichen woodlands in Grands-Jardins Provincial Park and Réserve fauniques des Laurentides in Quebec, Canada. A different letter above the bar denotes a significant difference between treatments, based on post hoc Scheffé tests.

was mainly dictated by web-building spiders and two hunting spiders, *T. terricola* and *Cybaeopsis tibialis* (Emerton) (Fig. 5; for locations of undisturbed sites see Fig. 4).

Discussion

Responses of spider assemblages to wildfire and clear-cutting

The main hypothesis was that wildfires and clearcuts disturb the structure and heterogeneity of the forest floor in different ways, leading to differences in ground-dwelling spider assemblages. Many forest-floor characteristics differed significantly between clear-cut and burned sites (Table 1). Likewise, the CA and CCA ordinations showed that the spider assemblages varied among treatments and the CCA ordination showed that spider assemblages associated with the different disturbance types responded to different environmental variables. Several of the environmental variables strongly associated with the CCA ordination axes, such as litter depth and percent cover of mosses and lichens, CWD, canopy cover, and ground vegetation, also differed significantly between burned and clear-cut sites. The amount of CWD (mainly logging residues), openness of the habitat, amount of exposed soil, and amount of dead needles covering the ground were the main forest-floor characteristics associated with the spider assemblages found in the clear-cut stands.

These forest-floor attributes are closely linked to the habitat requirements of hunting spiders and explain their significantly higher abundances in the clear-cut stands. The literature describes them as opportunistic spiders that hunt on open forest floors and rapidly colonize recently disturbed habitats (Uetz 1975; Aitchison-Bennell 1994). Other studies identify them as open-habitat specialists that are generally the dominant guild in recently logged areas (Huhta 1971; Coyle 1981; Jennings et al. 1988; Pajunen et al. 1995; Buddle et al. 2000). Spider assemblages from the burned sites were related to high percent cover of ground vegetation, low forest-floor heterogeneity, and deep litter resulting from the addition to the litter of an abundance of fire-killed moss–lichen substrate.

The stands recently disturbed by wildfires and clear-cutting

distribution and abundance of the dominant hunter species. Of the dominant spiders from each guild, the hunting spiders *Haplodrassus signifier* (C.L. Koch)*, P. hyperborea*, *P. mackenziana,* and the web-builders *Neoantistea agilis* (Keyserling)*, Tunagyna debilis* (Banks), and *Wabasso cacuminatus* Millidge were the most influential spiders in the ordination of the burned sites (Fig. 5; for locations of burned sites see Fig. 4). For the clearcuts, 4 species had a very strong influence on the ordination of the clear-cut sites: the hunters *P. moesta* and *P. uintana* and the web-builders *C. montana* and *S. montanus* (Fig. 5; for locations of clear-cut sites see Fig. 4). Two wolf spiders, *Arctosa alpigena* (Doleschall) and *P. xerampelina*, were dominant in both disturbance categories. The ordination of the undisturbed sites

Table 2. Measurements of alpha, beta, and gamma diversity of the spider assemblages found in undisturbed, burned, and clear-cut lichen woodlands of Grands-Jardins Provincial Park and Réserve Fauniques des Laurentides, Quebec.

	Alpha diversity			Beta diversity			Gamma diversity		
	Hunters	Web-builders	Total	Hunters	Web-builders	Total	Hunters	Web-builders	Total
Undisturbed	4.13±1.55a	7.23±0.67a	13.10±2.44a	2.17	2.03	1.04	18	39	57
Burned	4.22±0.61a	6.89±1.15a	9.54±1.60b	0.71	1.05	0.78	21	28	49
Clear-cut	3.73±0.46a	7.22±0.91a	8.60±1.34b	0.36	1.13	0.42	28	31	59

Table 3. Comparison of catch rates for the 10 most common spider species in each feeding guild using ANOVA (df = 2, 15).

	Undisturbed sites	Burned sites	Clear-cut sites	p
Hunters				
Alopecosa aculeata (Clerck)	13	33	10	ns
Arctosa alpigena (Doleschall)	0	10	14	0.049
Cybaeopsis tibialis Emerton	20	2	13	ns
Haplodrassus signifier (C.L. Koch)	2	4	6	ns
Pardosa hyperborea Thorell	76a	257b	84a	0.016
Pardosa mackenziana (Keyserling)	1b	72a	40a	<0.0001
Pardosa moesta Banks	1a	8a	233b	<0.0001
Pardosa uintana (Gertsch)	46a	170a	653b	0.001
Pardosa xerampelina (Keyserling)	1b	119a	152a	0.01
Trochosa terricola Thorell	20a	6b	11ab	0.037
Web-builders				
Cryphoeca montana Emerton	2a	0a	30b	<0.0001
Diplocentria bidentata (Emerton)	21	17	33	ns
Diplocentria rectangulata (Emerton)	16	3	4	ns
Neoantistea agilis (Keyserling)	0b	19a	8ab	0.012
Pocadicnemis americana Millidge	19a	24a	6b	0.038
Sisicottus montanus (Emerton)	21ab	1b	29a	0.033
Tunagyna debilis (Banks)	10	13	7	ns
Wabasso cacuminatus Millidge	3	14	0	ns
Walckenaeria directa (O. Pickard-Cambridge)	12	3	9	ns
Walckenaeria tricornis (Emerton)	9	13	5	ns

Note: Values followed by a different letter are significantly different between treatments, based on post hoc Scheffé tests. ns, not significant.

Table 4. Eigenvalues and percentages of total variance explained by each ordination performed in the study.

Ordination	Axis 1	Axis 2	Axis 3	Axis 4
CA				
Eigenvalue	0.3755	0.3092	0.2138	0.1737
% of total variance explained	22.2	18.2	12.6	10.3
CCA (Fig. 4)				
Eigenvalue	0.367	0.278	0.189	0.127
% of total variance explained	25.7	19.2	13.8	9.1
CCA (Fig. 5)				
Eigenvalue	0.334	0.238	0.087	0.07
% of total variance explained	34.6	25.3	11.5	7.6

Note: CA, correspondence analysis; CCA, canonical correspondence analysis.

are both newly created open habitats within the same forest ecosystem. Thus, the different forest-floor characteristics resulting from the two types of disturbance explain the differences in spider species composition between them, as indicated by our finding that species turnover was nearly twice as high among burned stands, and also by the CCA ordination. This confirms our prediction of higher heterogeneity of the species composition of forest spiders among burned stands than among clear-cut stands. Low species turnover in the clear-cut sites can be attributed to the fact that six species of

Fig. 4. Ordination of the 18 sites obtained from a canonical correspondence analysis (CCA) according to the spider assemblages (62 species) and environmental variables (12) measured at the sites. The values in parentheses show the percentage of variance explained by the canonical axis.
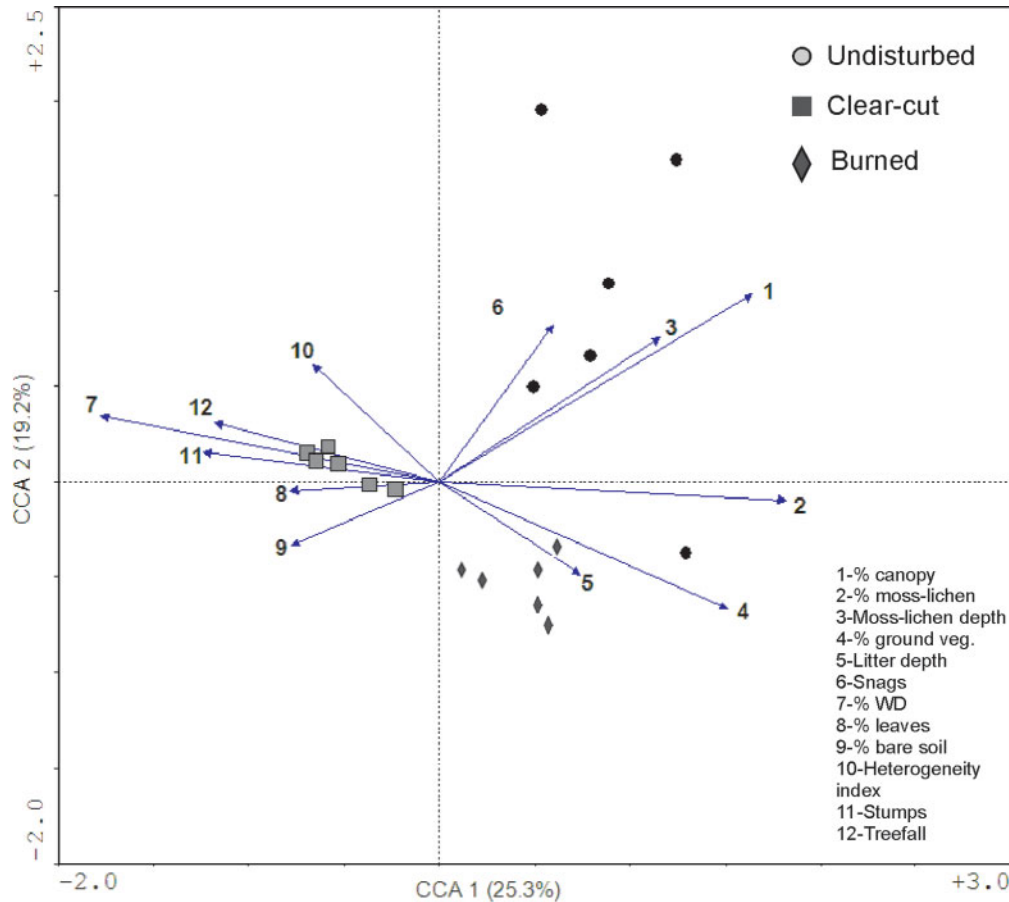
the genus *Pardosa* accounted for 84% of the total number collected and were found in every clear-cut site. The recurrence and numerical dominance of these species have a major effect on the species turnover that overshadows the species of web-builders that are found in the clearcuts.

However, within clear-cut sites, local forest-floor heterogeneity was high, owing to the presence of both bare ground and undisturbed patches of forest floor resulting from CPRS silvicultural operations. Nguyen-Xuan et al. (2000) also mentioned that CPRS leaves behind many patches of undisturbed forest floor to facilitate natural regeneration. These patches can contain a few spider species that are associated with mature undisturbed forest floors, which could explain why the clearcuts and control stands yielded the highest gamma-diversity values. This phenomenon was also mentioned by Huhta (1971), who noted that spider assemblages in recently clear-cut forest stands still show some characteristics of mature forest spider assemblages, owing to the persistence of some mature forest species that survive in remnants of mature forest microhabitats found in the recent clearcuts. In recently harvested sites in the boreal mixedwood forests of western Canada, Buddle et al. (2000) found a large increase in abundance of Linyphiidae, a family that is generally associated with mature forest stands (Huhta 1971; Coyle 1981; Pajunen et al. 1995). They attributed this in part to the possibility that these web-builders were able to survive by hiding deep in the litter. In the same area of Canada, Spence et al.

(1996) found that ground beetle (Carabidae) assemblages in recently harvested sites were also more similar to ground beetle assemblages in mature forests than to those found in older clear-cut sites, leading them to suggest that these "remnant" carabid species associated with mature forests would likely not persist in the cut landscape.

Species and guild-level responses

The species from the hunter and web-builder guilds showed different responses to environmental variables. Most web-builders were associated with variables pertaining to mature forest stands, like canopy cover, the moss–lichen component on the forest floor, and dense ground-vegetation cover, which they require to attach their webs (Huhta 1971; Palmgren 1977). Hunting spiders were associated with variables representing openness of the forest floor, such as high percentages of exposed soil and dry coniferous needles, and in the case of burned habitats a high percentage of burned litter. These forest-floor characteristics facilitate prey hunting and egg sunning for lycosid females (Coyle 1981; Buddle 2001). It has been suggested that their morphology (Coyle 1981) and larger body size are adaptations for enduring the larger temperature variations that occur in open habitats. The hunter guild was the main group of species responsible for the differences in catch rates and in species composition of the assemblages found in clearcuts and burned sites. We suggest that the larger amounts of fallen CWD (mainly logging resi-

Fig. 5. Canonical correspondence analysis of the 10 most commonly collected spider species from the hunter guild (▲) and the web-builder guild (○). The arrows represent the environmental variables, while their length indicates the importance of their effect on the spider species. Species are denoted as follows: aloacu, *Alopecosa aculeata*; arcalp, *Arctosa alpigena*; crymon, *Cryphoeca montana*; cybtib, *Cybaeopsis tibialis*; dipbid, *Diplocentria bidentata*; diprec, *Diplocentria rectangulata*; hapsig, *Haplodrassus signifer*; neoagi, *Neoantistea agilis*; parhyp, *Pardosa hyperborea*; parmac, *Pardosa mackenziana*; parmoe, *Pardosa moesta*; paruin, *Pardosa uintana*; parxer, *Pardosa xerampelina*; pocame, *Pocadicnemis americana*; sismon, *Sisicottus montanus*; troter, *Trochosa terricola*; tundeb, *Tunagyna debilis*; wabcac; *Wabasso cacuminatus*; waldir, *Walckenaeria directa*; waltri, *Walckenaeria tricornis*.
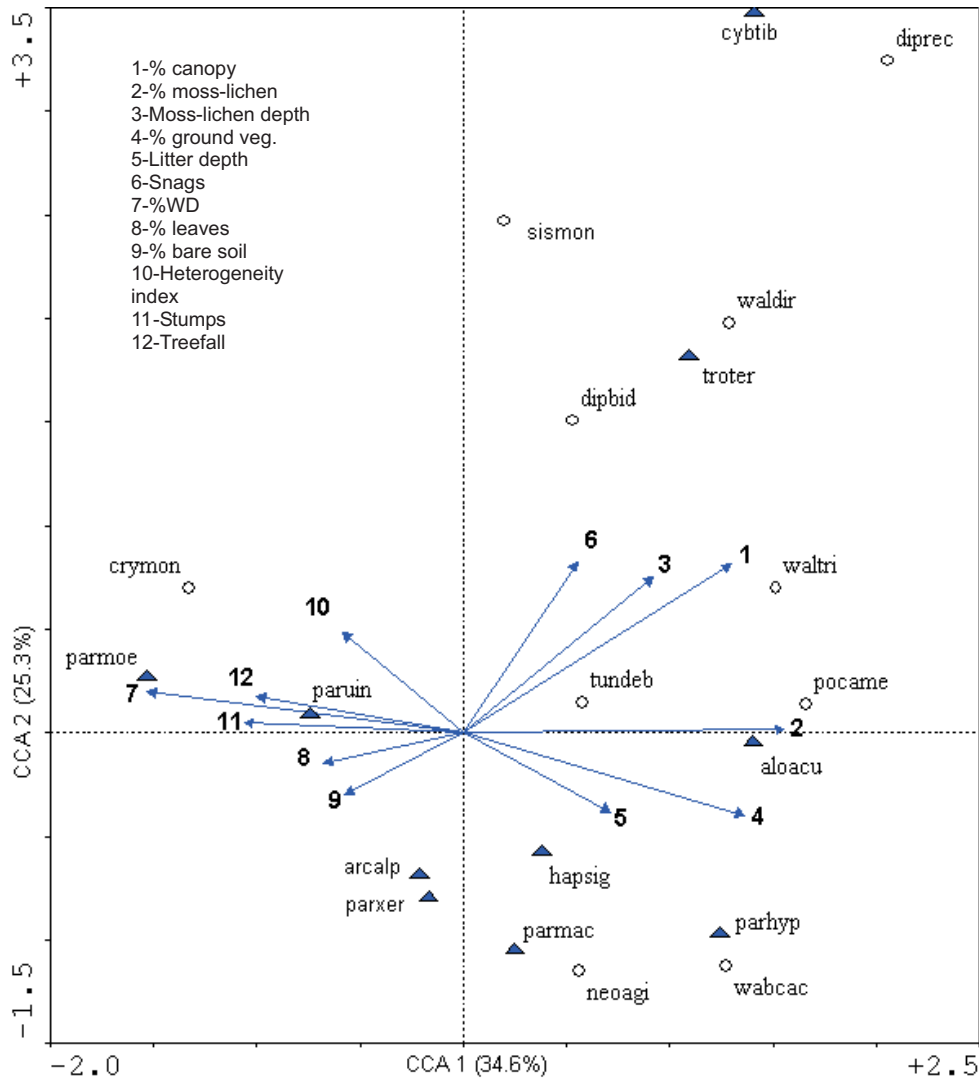
dues) found in our clear-cut stands could be related to the differences in spider species composition and mean species richness, as females of some wolf spiders are known to stand preferentially on fallen wood to sun their egg sacs (Vlijm et al. 1963; Buddle 2001). This could explain in part why *P. moesta* and *P. uintana* were significantly more abundant in clear-cut sites, and why wolf spiders were more species-rich and twice as abundant in clear-cut sites.

The web-building spiders *W. cacuminatus*, and *W. minuta* and the hunting spiders *P. hyperborea* and *Alopecosa aculeata* (Clerck) were found mainly in burned stands. This indicates that wildfires create forest-floor characteristics that are rarer or absent in clearcuts, like a denser shrub cover, abundant desiccated moss–lichen substrate still covering the ground, charcoal, and a thicker litter layer. More information on the ecology of *W. cacuminatus* and *W. minuta* is needed to deter-

mine which habitat variables are responsible for their affinity with burned stands. As for hunting spiders, Buddle et al. (2000) also reported significantly higher captures of *P. hyperborea* in recently burned trembling aspen, *Populus tremuloides* Michx., stands in western Canada, and suggested that *P. hyperborea* were recolonizing the burned stands from unburned black spruce bogs in the landscape. Buddle et al. (2000) and Koponen (1993) also suggested that the wolf spider species *A. alpigena* and *Pirata bryantae* Kurata are aided by conditions that prevail after a wildfire. In contrast, these two species were found in similar numbers in our harvested and burned stands and are clearly not "fire-dependent". However, wildfire clearly creates habitats characteristics that current harvesting approaches in the boreal forests do not provide. This argues in favor of altering forest-harvesting approaches to produce conditions that benefit these species.

Although most spider species responded in accordance with the general habitat characteristics reported in the literature for their guilds, *T. terricola*, a hunting spider, was found mainly in undisturbed forests and the web-building spiders *C. montana* and *N. agilis* were found mostly in open habitats and portrayed habitat preferences contrary to those generally recognized for their guilds. This indicates that generalizations about the habitat affinities of spider guilds, while very informative, do not hold for all species within the guilds.

Conclusion

We found that forest stands that were recently clear-cut using methods that protect the soil did not yield ground-dwelling spider assemblages similar to those found in recently burned stands. These results are in accordance with other studies that have shown differences in the effects of wildfire and wood harvesting on biotic and abiotic components of boreal ecosystems (Johnston and Elliott 1996; Imbeau et al. 1999; Carignan et al. 2000; Nguyen-Xuan et al. 2000; Simon et al. 2002). Our study is one of the few to show that logging produces more homogeneous disturbance at the landscape level, thereby producing very similar spider assemblages across the landscape compared with wildfire. We also provide new and detailed correlative information on the response of spider assemblages shortly after both types of perturbation and how this response is associated with the forest-floor structure left by each disturbance at the assemblage level and the spider level. This is important, since the natural disturbance regime of the boreal forest creates a mosaic of stands at various stages of succession, and the presence of each stage of succession across the landscape is essential for completion of the life cycle of many species. Thus, increasing the similarity of the patterns and processes of the disturbances created by recent clearcuts to those created by recent wildfires is essential to provide early-successional stands to which the boreal fauna is adapted. We consider that understanding the differences between stands recently disturbed by logging and wildfire is as critical as knowing whether the communities found after both types of disturbance converge over a harvesting cycle for the reasons mentioned above.

In view of this, our results suggest several measures for increasing the similarity of spider assemblages in clear-cut and burned areas. Most importantly, clear-cutting practices that maintain more ground vegetation and deeper litter are needed. In addition, prescribed burning in clear-cut stands may reduce the differences between burned and clear-cut stands. Finally, the higher spider species turnover among burned stands than among clear-cut stands suggests that harvesting techniques should be diversified to enhance environmental differences among harvesting blocks, to increase the spider species turnover among harvested stands.

Acknowledgments

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Appendix A

Appendix appears on the following page.

Table A1. Data matrix (number of individuals per trap per week) of the spider species collected at each site during the study.

	Con1	Con2	Con3	Con4	Con5	Con6	Burn1	Burn2	Burn3	Burn4	Burn5	Burn6	Cut1	Cut2	Cut3	Cut4	Cut5	Cut6
Agroeca ornata Banks	0	0	0	0.08	0	0	0	0	0	0.111	0	0	0	0	0	0	0	0
Agyneta allosubtilis Loksa	0	0	0	0	0	0	0	0	0	0	0	0	0	0.111	0.056	0	0	0
Agyneta olivacea (Emerton)	0	0	0	0	0	0	0	0	0	0	0	0.056	0	0.056	0	0	0	0
Agyneta simplex (Emerton)	0.133	0	0.118	0	0	0	0	0	0.056	0	0	0	0	0	0	0	0.167	0.278
Alopecosa aculeata (Clerck)	0.133	0.571	0.353	0	0	0.056	0.222	0.353	0.278	0.167	0.611	0.222	0.111	0	0	0	0	0.278
Aphileta misera (O. Pickard-Cambridge)	0	0	0	0	0	0	0	0	0	0	0	0	0.111	0	0	0	0	0
Arctosa alpigena (Doleschall)	0	0	0	0	0	0	0.056	0.176	0	0.167	0.111	0.056	0.222	0	0.333	0.111	0.111	0
Arctosa raptor (Kulczyński)	0	0	0	0	0	0	0	0	0	0	0	0	0.111	0	0.111	0.056	0	0
Bathyphantes pallidus (Banks)	0.067	0	0	0	0	0	0	0	0	0	0	0	0	0	0.111	0.111	0.056	0
Callobius bennetti (Blackwall)	0	0	0	0.25	0	0.111	0	0	0	0.056	0	0	0	0.056	0	0	0	0
Carorita limnaea (Crosby & Bishop)	0.2	0	0	0	0.333	0	0.056	0	0	0	0	0	0	0	0	0	0	0
Centromerus furcatus (Emerton)	0	0	0	0	0.333	0	0	0	0	0	0	0	0	0	0	0	0.111	0
Centromerus longibulbus (Emerton)	0	0	0.176	0.083	0	0	0	0	0.111	0	0	0	0	0	0	0	0	0
Ceratinella brunnea Emerton	0.067	0	0	0	0.056	0.056	0	0.059	0	0	0	0.111	0	0.056	0	0.111	0	0.111
Cicurina brevis (Emerton)	0	0	0	0	0	0	0	0	0	0	0	0	0	0.056	0	0	0	0
Clubiona canadensis Emerton	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.056	0	0	0
Clubiona kulczinskii de Lessert	0	0	0	0.083	0	0	0	0	0	0.056	0	0	0	0	0	0	0	0
Cnephalocotes obscurus (Blackwall)	0	0	0	0	0	0	0	0	0.112	0.116	0	0	0	0	0	0	0	0
Cryphoeca montana Emerton	0.067	0	0	0.25	0	0.056	0	0	0	0	0	0	0.167	0.167	0.5	0.444	0.056	0.333
Cybaeopsis tibialis (Emerton)	0.267	1	0	0.167	0.111	0.222	0	0.059	0.056	0	0	0	0.222	0.111	0.111	0.111	0.111	0.056
Diplocentria bidentata (Emerton)	0.267	0.429	0.118	0	0.222	0.333	0.722	0.118	0	0.056	0.056	0	0.222	0.111	0.333	0.5	0.389	0.278
Diplocentria rectangulata (Emerton)	0.6	0.714	0	0	0.056	0.056	0.056	0	0	0.056	0.056	0	0	0	0.111	0	0.111	0
Drassodes neglectus (Keyserling)	0	0	0	0	0	0	0	0	0	0.111	0	0	0	0	0	0	0	0
Enoplognatha intrepida (Sørensen)	0	0	0	0	0	0	0	0	0	0.056	0	0	0	0	0	0	0	0
Erigoninae sp. 1	0	0	0	0	0	0.056	0	0	0	0	0	0	0	0	0	0	0	0
Euryopis argentea Emerton	0	0	0.176	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gnaphosa microps Holm	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.056	0	0	0
Gnaphosa muscorum (L. Koch)	0	0	0	0	0	0	0.167	0.059	0	0.056	0	0	0	0.056	0.056	0	0.056	0.056
Gonatium crassipalpum Bryant	0	0	0	0	0	0.056	0	0	0	0	0	0	0	0	0	0	0	0
Hahnia cinerea Emerton	0	0	0	0	0	0	0.056	0	0	0	0	0	0	0	0	0	0	0
Halorates plumosus (Emerton)	0	0	0	0	0	0	0	0	0	0	0	0	0.056	0	0	0	0	0
Haplodrassus eunis Chamberlin	0	0	0	0	0	0	0	0	0.056	0	0	0	0	0	0	0	0	0
Haplodrassus hiemalis (Emerton)	0	0	0	0	0	0	0	0	0	0	0	0	0	0.056	0	0	0	0
Haplodrassus signifer (C.L. Koch)	0	0	0.118	0	0	0	0.056	0	0	0	0.056	0.111	0.056	0.056	0	0.116	0.056	0.056
Hilaira herniosa (Thorell)	0	0	0	0	0.056	0	0	0	0	0	0	0	0	0	0	0	0	0
Hybauchenidium gibbosum (Sørensen)	0.07	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Improphantes complicatus (Emerton)	0.133	0.143	0	0.083	0.056	0	0	0.059	0	0	0	0	0	0	0	0	0	0
Lepthyphantes alpinus (Emerton)	0	0	0	0	0.056	0.056	0	0	0	0	0	0	0.056	0	0.111	0.167	0	0
Maro amplus (Dondale & Buckle)	0.133	0.143	0	0	0	0.056	0	0	0	0	0	0	0	0	0.056	0	0	0
Micaria aenea Thorell	0	0	0.118	0	0	0	0	0.059	0.111	0	0	0	0	0	0	0	0	0
Micaria pulicaria (Sundevall)	0	0	0	0	0	0	0	0	0	0.056	0	0	0	0	0	0.056	0	0.056
Micrargus longitarsus (Emerton)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.056	0	0
Neoantistea agilis (Keyserling)	0	0	0	0	0	0	0.222	0.176	0.167	0.111	0	0.389	0.111	0	0	0.056	0.056	0.222
Oreonetides vaginatus (Thorell)	0	0	0	0	0	0	0	0	0	0	0	0	0.056	0	0.111	0	0	0
Oreophantes recurvatus (Emerton)	0	0	0	0	0	0.056	0	0	0	0	0	0	0	0	0.056	0	0	0
Pardosa concinna (Thorell)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.111	0.167
Pardosa hyperborea Thorell	1.267	0.571	2.941	0.083	0	0.111	2.889	2.588	4.444	2	1.389	1.111	0.722	0.444	0.833	1	0.722	0.944

Table A1 (continued).

	Con1	Con2	Con3	Con4	Con5	Con6	Burn1	Burn2	Burn3	Burn4	Burn5	Burn6	Cut1	Cut2	Cut3	Cut4	Cut5	Cut6
Pardosa mackenziana (Keyserling)	0	0	0.059	0	0	0	0.667	0.882	0.667	0.444	1.056	0.333	0.167	0.556	0.667	0.611	0.111	0.111
Pardosa moesta Banks	0.07	0	0.059	0	0	0	0.056	0.118	0	0.056	0.056	0.167	1.167	4.222	2.667	2.333	0.778	1.778
Pardosa uintana Gertsch	1	1.143	0.118	0.083	0.778	0.333	0.889	4.294	0.389	0.778	2.556	0.778	2.889	5.278	5.722	5.389	5.056	11.944
Pardosa xerampelina (Keyserling)	0	0	0	0	0	0.056	1.556	2.176	0.944	1.333	0.5	0.222	3.222	1.944	0.889	0.889	0.444	1.056
Pardosa fuscula (Thorell)	0	0	0	0	0	0	0	0	0	0	0	0	0.278	0	0	0.056	0	0
Pellenes montanus (Emerton)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.056	0	0
Philodromus placidus Banks	0.07	0	0	0.083	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pirata bryantae Kurata	0	0	0	0	0.056	0	0	0	0	0	0	0.056	0	0	0	0	0	0.056
Pirata minutus Emerton	0	0	0	0	0	0	0	0	0	0	0	0	0	0.06	0	0	0	0
Pirata montanus Emerton	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.056
Pirata piraticus (Clerck)	0	0	0	0	0	0	0	0	0	0	0	0	0.111	0	0	0	0	0
Pityohyphantes costatus (Hentz)	0	0	0.059	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pocadicnemis americana Millidge	0.2	0.286	0.529	0.083	0.222	0	0.278	0.176	0.111	0.278	0.278	0.222	0	0	0.111	0.056	0.111	0.056
Robertus fuscus (Emerton)	0.07	0.143	0	0	0	0	0	0	0.056	0	0	0	0.056	0.167	0	0	0	0
Sciastes truncatus (Emerton)	0.333	0	0	0	0	0	0	0	0.056	0	0	0	0.111	0.167	0	0	0.056	0
Scironis tarsalis (Emerton)	0	0	0.083	0.083	0.056	0	0.056	0	0	0	0	0	0	0	0	0	0	0
Scotynotilus pallidus (Emerton)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scotynotilus sacer (Crosby)	0	0.143	0	0	0	0	0.056	0	0	0	0	0	0	0	0.056	0	0	0
Sisicottus montanus (Emerton)	0.4	0	0.059	0.5	0.111	0.333	0.056	0	0	0	0	0	0.167	0.056	0.5	0.444	0	0.389
Sisis rotundus (Emerton)	0	0	0	0	0	0	0	0	0	0	0	0	0.056	0	0	0	0	0
Linyphiidae sp. 64*	0	0	0	0.167	0.056	0	0	0.059	0	0	0	0	0	0	0	0	0	0.056
Styloctetor stativus (Simon)	0	0	0.059	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tapinocyba bicarinata (Emerton)	0.07	0	0	0	0	0	0.056	0	0	0	0	0.056	0	0	0	0	0	0
Tapinocyba simplex (Emerton)	0.07	0	0	0	0	0	0	0	0.056	0	0	0	0	0	0	0	0	0
Tetragnatha viridis Walckenaer	0	0	0	0	0	0	0.056	0	0	0	0	0	0	0	0	0	0	0
Theonoe stridula Crosby	0	0	0	0	0	0	0.056	0	0	0	0	0	0	0	0	0	0	0
Trochosa terricola Thorell	0.2	0.143	0.353	0.083	0.111	0.389	0	0.235	0	0.167	0	0	0.167	0.111	0.111	0.111	0.056	0.056
Tunagyna debilis (Banks)	0	0	0.059	0	0.5	0	0.111	0.176	0.056	0	0.111	0.111	0.167	0.111	0	0	0.111	0
Walckenaeria arctica Millidge	0.133	0	0	0	0	0	0	0	0.111	0	0	0	0	0	0	0	0	0
Walckenaeria atrotibialis (O. Pickard-Cambridge)	0	0	0.083	0.083	0	0.056	0	0.059	0	0.056	0.056	0	0	0	0	0	0	0
Walckenaeria castanea (Emerton)	0	0	0	0	0	0	0.111	0	0.056	0	0	0	0	0	0	0	0	0
Walckenaeria clavipalpis Millidge	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.056	0	0
Walckenaeria directa (O. Pickard-Cambridge)	0.4	0.286	0.118	0.083	0	0.056	0	0.059	0	0.056	0.056	0	0.056	0.111	0.167	0.056	0.111	0
Walckenaeria fallax Millidge	0	0	0	0	0	0.056	0	0	0	0	0	0	0	0	0	0	0	0
Walckenaeria karpinskii (O. Pickard-Cambridge)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.056	0
Walckenaeria minuta (Emerton)	0	0	0.059	0	0	0	0.111	0.529	0.111	0.056	0.056	0	0	0	0	0	0	0
Walckenaeria tricornis(Emerton)	0.333	0.286	0.059	0	0.056	0.056	0.056	0.294	0.111	0.111	0.056	0.111	0.056	0.286	0	0	0.167	0.056
Wabasso cacuminatus Millidge	0.2	0	0	0	0	0	0.056	0.706	0	0.056	0	0	0	0	0	0	0	0
Wubana pacifica (Banks)	0	0	0	0	0.056	0.056	0	0	0	0	0	0	0	0	0	0	0	0
Xysticus britcheri Gertsch	0	0	0	0	0.056	0	0	0	0	0	0	0	0	0.056	0	0	0	0
Xysticus canadensis Gertsch	0.133	0	0	0	0	0.056	0	0	0	0	0	0	0.056	0.056	0	0	0.056	0
Xysticus ellipticus Turnbull, Dondale & Redner	0	0	0	0	0	0	0	0	0	0.056	0	0	0	0	0.056	0	0	0
Xysticus luctuosus (Blackwall)	0	0	0.06	0	0	0	0	0	0	0	0	0.111	0	0	0	0	0	0

Table A1 (*concluded*).

	Con1	Con2	Con3	Con4	Con5	Con6	Burn1	Burn2	Burn3	Burn4	Burn5	Burn6	Cut1	Cut2	Cut3	Cut4	Cut5	Cut6
Xysticus obscurus Collett	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.056	0
Zelotes fratris Chamberlin	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.056	0	0	0.056
Zornella cultrigera (L. Koch)	0.07	0	0	0	0	0	0	0	0	0.056	0	0	0	0	0	0.056	0	0

*Undescribed species 64 from the Canadian National Collection at Agriculture and Agri-Food Canada.