

Edge effects created by wildfire and clear-cutting on boreal forest ground-dwelling spiders

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Abstract

The response of ground-dwelling spider assemblages to edges created by wildfire was compared to their response to clear-cut edges in black spruce forests in eastern Canada. For each disturbance six edge transects 100 m long were established. Spiders were collected with pitfall traps 10 m apart from 50 m inside the disturbances to 50 m in the forest interior. Measurements of the forest floor structure and the habitat around the traps were also taken. Most habitat variables varied similarly across both wildfire and clear-cut edges but two variables, coarse woody debris and shrub cover changed more abruptly at edges of clear-cuts than at wildfire edges. Two separate CA analyses of the burned and clear-cut edge transects showed that changes in spider community species composition were more abrupt at clear-cut edges than at burn edges. A species indicator analysis (INDVAL) was used to identify species that were significantly associated with specific edge zones. Eight species were significantly associated with open (disturbed) habitats, one species was significantly associated with both burned and clear-cut edges, and four species were significantly associated with the forest interior. *T*-tests of slope coefficients from separate simple regressions of abundance and richness over distance showed that open habitat specialist's abundance and richness changed significantly more abruptly at clear-cut edges than at wildfire edges. Locally weighted smoothed regressions showed that the extent of edge influence on ground-dwelling spider guilds (open habitat and forest interior specialist) penetrated 20–30 m into the disturbances, 30 m into the forest interior at clear-cut edges, and at least 50 m into the forest interior for wildfire edge transects. Our results suggest that a minimum width of 100 m is necessary to maintain characteristics of forest interior spider assemblages in forest remnants, riparian or road buffers, and forest strips between cut-blocks.

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1. Introduction

Wildfire and forest harvesting, in the form of large-scale clear-cutting, represent major disturbances to boreal forests in North America (Bergeron et al., 2002; Rees and Juday, 2002). Recently burned or harvested stands differ from mature forests in many obvious ways, such as openness, light distribution, humidity, temperature, wind, and overall microclimate stability (Forman, 1995; deMaynadier and Hunter, 1998; Larrivée et al., 2005). The contrast between

burned and logged areas and the adjacent forest interior creates an “induced edge” (Laurance and Yensen, 1991; Voller and Harrison, 1998). The edge is defined as the part of both cover types that is modified, both for biotic and abiotic components, through its interactions with the adjacent cover type (Murcia, 1995; Hilmo and Holien, 2002). Clear-cuts can create hard or abrupt edges while wildfires create softer edges (Laurance, 1991; Forman, 1995; Voller and Harrison, 1998; Harper et al., 2004). A hard edge creates an abrupt transition between the two cover types with very limited penetration of edge effect into the adjacent cover type, while a soft edge is more permeable to edge effects, which penetrate farther into the adjacent cover type (Forman, 1995; Voller and Harrison, 1998; Harper et al., 2005). As such, edge effects occurring at edges from wildfires and clear-cutting may lead to different ecological changes at the interface between the disturbed and undisturbed cover types.

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Sustainable management efforts of the boreal forest aim to adjust and improve forestry practices towards patterns and processes that are close to those generated by natural disturbance regimes (Anglestam, 1998; Attiwill, 1994; Bergeron et al., 2001; Simberloff, 2001; Bergeron et al., 2004). Thus, determining if the ecological changes are different and how they affect the fauna on both sides of the edge are essential. From a landscape conservation perspective, measuring edge effects on species associated with interior forest conditions will better assess the impact of silvicultural practices on the landscape and organisms (Murcia, 1995; Baker et al., 2007).

The depth of edge influence (DEI) (Harper and MacDonald, 2001; Ries et al., 2004) on most microclimatic variables in the forest interior generally vanishes within 60 m of the edge (Matlack, 1993; Murcia, 1995; Davies-Colley et al., 2000; for up to 250 m, see Chen et al., 1995). The DEI can also affect the microclimate 20 m into the open area (Cadenasso et al., 1997; Davies-Colley et al., 2000). The responses of invertebrates to edge effects are generally detected 100 m from the edge inside the habitat (Murcia, 1995; Spence et al., 1996; Didham et al., 1998; Baker et al., 2007) while the DEI on plants is generally less than 100 m (Jules, 1998; Esseen and Renhorn, 1998; Rheault et al., 2003; Ries et al., 2004).

Several studies have investigated edge effects created by timber harvesting on ground-dwelling beetles (Spence et al., 1996; Heliola et al., 2001; Phillips et al., 2006; Baker et al., 2007) and spiders (Pearce et al., 2005), but to our knowledge no empirical studies have compared edge effects resulting from wildfires and logging on spiders in the boreal forest. Better knowledge of the difference between organisms' response to anthropogenic versus naturally induced edges is important in the context of the increasing density of clear-cut edges in boreal landscapes. Such information is needed to determine if improved forestry practices through creating spatial and temporal patterns that are close to those generated by natural disturbance regimes is indeed efficient for arthropods (Buddle et al., 2006).

Many attributes of spiders (Arachnida: Araneae) make them a good taxon for the investigation of edge effects. They have high abundances (Buddle et al., 2000; Coddington et al., 1996; Coyle, 1981; Huhta, 1971; Jennings et al., 1988). Species richness and individual species abundances and distributions can be associated to structural attributes and abiotic features found in their habitats (Hatley and Macmahon, 1980; Uetz, 1979). They are important components of food chains (Atlegrim and Sjöberg, 1995; Nyffeler, 2000), and are involved in nutrient recycling and fixation in early stages of succession in disturbed areas (Hodkinson et al., 2001). Also, spiders can be grouped into guilds of open or interior habitat specialists or generalists.

In this paper we compare edge effects created by a recent wildfire and recent clear-cuts on the ground-dwelling spider assemblages in a boreal forest. We have previously shown that ground-dwelling spider assemblages in a boreal forest differ between a recent wildfire and recent clear-cuts (Larrivé et al., 2005). Here, we hypothesize that environmental conditions at the edges resulting from wildfires are different from those

generated by clear-cuts and consequently create different DEI's (Ries and Sisk, 2004) on ground-dwelling spider assemblages associated with edges created by the two disturbance types. More specifically, our predictions are: (1) environmental variables along edges resulting from clear-cuts change more abruptly than along edges of wildfire (Harper et al., 2005); and (2) this results in a shorter DEI response of habitat specialist spiders across clear-cuts edges than across wildfire edges (Ries and Sisk, 2004).

2. Methods

2.1. Study area and sampling

The study was conducted during the summer of 2001 in the Park des Grands-Jardins (the "park") (47°41'N–70°41'W) and in the Réserve Faunique des Laurentides (the "reserve"), both located in the Charlevoix region, 150 km north east of Québec City, Canada (Fig. 1). For both the park and the reserve, Black Spruce (*Picea mariana* (Mill)) was the dominant tree species with Balsam Fir (*Abies balsamea* (L.)) being the sub-dominant species. The ground vegetation was dominated by dwarf shrubs such as *Ledum groenlandicum* Retzius, *Salix* sp., *Vaccinium angustifolium* Ait., *V. vitis-idea* L. and *Kalmia angustifolia* L. The ground layer is dominated by sphagnum mosses and *Cladonia* sp. is also common. In late spring of 1999, a 5197 ha area of the park burned during a highly intense wildfire. During the same period, several sites in the reserve were clear-cut using the "clear-cutting with regeneration and soil protection" (CRSP) approach. This practice consists in harvesting all commercial timber in a stand but protecting advanced regeneration and minimizing disturbance to soils. Hence, saplings and small trees are not harvested, leaving some vertical structure within harvested stands.

In the spring of 2001, twelve 100 m transects (six in burn and six in clear-cut treatments) were set up perpendicular to clear-cuts and burns edges and extended into remnant mature forests (Fig. 1). They were located 50 m within the disturbance and extended 50 m inside the forest interior. There was one pitfall trap (10 cm in diameter) every 10 m for a total of 11 traps along each transect. The 10 m distance between traps is short enough to detect changes in spiders assemblages along the sampling transects (Digweed et al., 1995). The traps were inserted in the ground with the rim of the traps flush with the ground. Each trap was composed of two plastic cups, one within the other, to facilitate the removal of the inner cup while minimizing disturbance to the soil surrounding the trap. In each trap we poured 100 ml of a 50% ethylene glycol solution and a few drops of soap. A square 10 cm by 10 cm plastic roof supported by nails was placed 5 cm above the traps. Traps were active for 6 weeks from June 6th, 2001 to July 17th, 2001. This sampling period covered the first peak in activity for most boreal-forest spider families (Aitchison-Benell, 1994; Niemela et al., 1994; Buddle, 2000; Buddle and Draney, 2004). It thus allowed to grasp the main structure of ground-dwelling spider assemblages and draw inferences on the spider community's response to wildfire and harvesting (see Larrivé et al., 2005). All traps

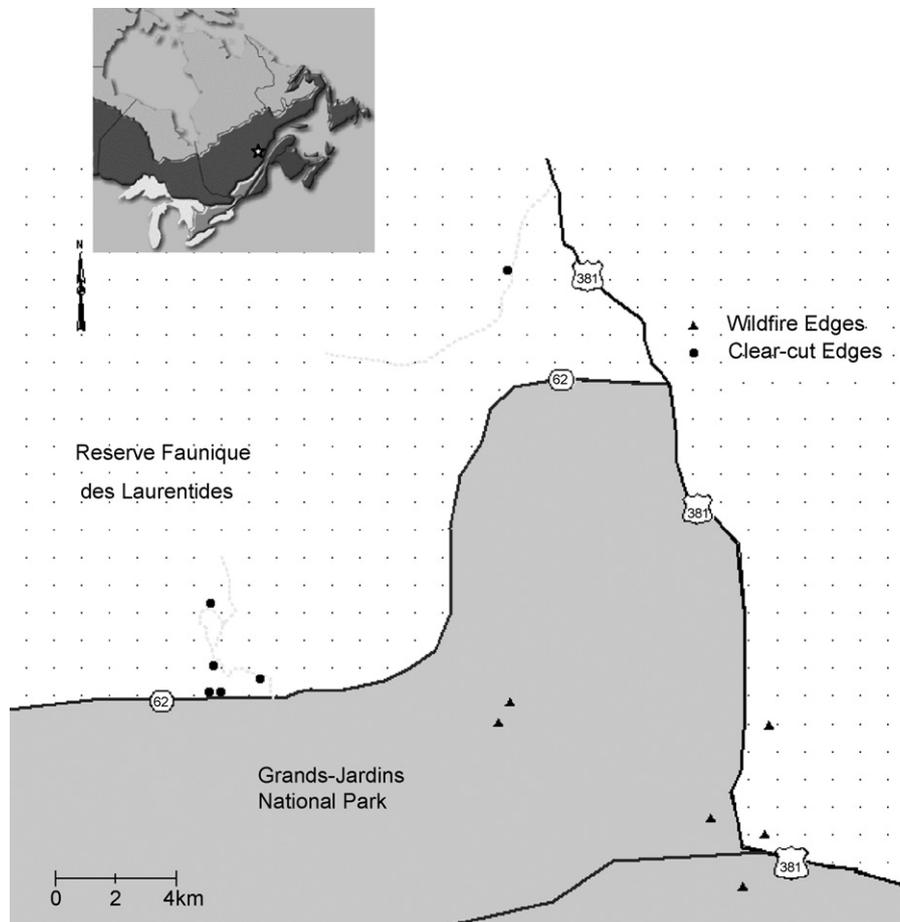


Fig. 1. Location of the sampling sites in the Grands-Jardins National Park and the Réserves Faunique des Laurentides in Québec, Canada.

were emptied weekly. To account for traps damaged during the sampling period, abundance and richness values were converted to values per trap per week. When possible, all adult spiders and juveniles were identified to species using appropriate literature, and compared with specimens from the National Collection at Agriculture Canada in Ottawa. Classification followed Platnick's (2007) *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.

2.2. Habitat structure

Besides each trap, environmental conditions on ground were sampled within 1 m² quadrats. In each quadrat, we measured litter depth, and the percent cover on the ground of moss-lichen substrate, bare soil, leaves (needles), shrubs, and coarse woody debris (CWD) which included logging residues in the clear-cut transects. We also measured tree canopy cover following the site tube procedure of James and Shugart (1970) with the exception that measurements were taken every metre for 10 m in each cardinal direction. These values were then converted into an overall percentage of canopy cover.

2.3. Data analysis

To detect changes in the environmental conditions along our edge transects, a locally weighted regression smoothing procedure (LOWESS, tension $\alpha = 0.5$, Legendre and Legendre, 1998; deMaynadier and Hunter, 1998) was conducted with SYSTAT 10[©] (Wilkinson et al., 1992) of each environmental variable on distance along transects in each of the two disturbance types. In a LOWESS analysis, a tension of $\alpha = 0.5$ represents the proportion of the data in the regression used to obtain every smoothed value. A LOWESS procedure is obtained by a weighted linear least squares regression.

To test for differences in the abruptness of the changes in our environmental variables at the wildfire and clear-cut edges a *t*-test was performed to compare the 12 slope coefficients (six from burned edge transect and six from clear-cut edge transects) obtained through simple regressions of each variable on distance along each transect. We apply logic and reason to interpret our multiple *t*-test comparisons as the sequential Bonferroni adjustment can increase greatly the number of Type II error rate compared to the increase of Type I error rate without adjustment (Moran, 2003). Thus, we are afraid that multiple test adjustments could make us fail to observe a difference when in truth there is one.

To assess changes in species composition of spider assemblages with regards to edge types, we conducted separate correspondence analyses (CA) (Ter Braak, 1986; Ter Braak and Smilauer, 1998; Legendre and Legendre, 1998) for spider data sets from the wildfire transects and the clear-cut transects, respectively. We chose CA because our undisturbed and disturbed sites provide a large environmental gradient, offering a high chance of covering the species' low and optimal frequencies.

To facilitate the interpretation of the CA biplots, Gaussian bivariate ellipses representing three distance categories from our edge transects were superimposed on the ordinations using SYSTAT 10[®]. Each ellipse is centered on the sample means of the axis 1 and 2 loadings of the samples composing a distance category and represents one standard deviation from the sample's mean loadings (Wilkinson et al., 1992). The distance categories were *cut* or *burned* (50–20 m in the disturbance), *edge* (10 m in the disturbance to 10 m in the forest interior) and *interior* (20–50 m in the forest interior). Canonical correspondence analyses were then performed on the two data sets to determine the combination of environmental variables that were associated with the spider CA ordination axes (Ter Braak and Smilauer, 1998).

An indicator species analysis (Dufrêne and Legendre, 1997) was performed with PC-ORD (McCune and Mefford, 1999) to detect species significantly associated with the three habitat zones as defined in the CA. The indicator value (IV) calculated for each species works as follow: 0 designates no association and 100 represents a complete indicator value to a certain habitat. The indicator value is made of the species relative abundance and frequency in each of the zones (Magura et al., 2001; McGeoch et al., 2002). Our analysis was based on species catch rates (ind/trap/week) in each zone for each transect. The statistical significance of the IV's obtained was tested with a Monte Carlo randomization procedure (1000 permutations). Species are deemed characteristic of a zone when $IV > 25\%$ and significant (p -value < 0.05) (Dufrêne and Legendre, 1997).

To measure and compare the depth of edge influence (DEI) into the forest interior and disturbed areas, we used the subset of spider species identified "edge zone species" by our indicator species analysis. The catch rates of each species within each group of species (open habitat and interior habitat) were then summed for each distance along our edge transects. Species identified by Larrivé et al. (2005) as significantly associated with forest interior, burned habitats or clear-cut habitats but that were marginally indicator species according to INDVAL were included in their appropriate edge zones. Species richness of each group was also calculated for each trap. We used a locally weighted regression smoothing procedure (Wilkinson et al., 1992) (LOWESS, tension = 0.5, Legendre and Legendre, 1998; deMaynadier and Hunter, 1998) similar to the one performed for the environmental variables to locate and compare responses in abundances and richness of open and interior habitat spiders to the two types of edges.

Differences in the abruptness of the changes in spider abundance at wildfire and clear-cut edges were assessed using t -

tests on the slope coefficients obtained through simple linear regressions of spider abundance on distance along each transect. The same procedure was repeated for the species richness of each group. Here as well, we used logic and reasonable interpretation of our experimental design for the interpretation of the multiple p values obtained from our t -tests in lieu of a sequential Bonferroni. The Bonferroni adjustment would have forced us to reject many tests all significant prior to adjustment which is contrary to logic as demonstrated by Moran (2003).

3. Results

Altogether 6222 individuals of 124 species from 67 genera and 15 families were captured. The wildfire transect samples contained 97 spider species and 2649 individuals, while 86 species and 3573 individuals were found in the clear-cut transects. Hunting spider species from the genus *Pardosa* (Araneae: Lycosidae) were numerically dominant throughout both the wildfire (1301 individuals) and the clear-cut (2072 individuals) edge transects. Web-building spiders Linyphiidae (Linyphiinae and Erigoninae) had the highest species richness in both the burned edges and the clear-cut edges, with 49 species and 47 species, respectively, while Lycosids (hunting spiders) had the second highest species richness, with 12 species in the wildfire edges and 13 species in the clear-cut edges.

3.1. Changes in forest floor attributes and vegetation across the edges

Changes in environmental conditions generally occurred from 30 m in the disturbed area to 30 m in the forest interior section of transects (Fig. 2). The only variable that did not change at the edges was the percentage of leaves on ground. The percent cover of shrubs, coarse woody debris, and exposed soils differed in their responses to clear-cut and wildfire edges. The percent cover of coarse woody debris changed minimally across the wildfire edges but showed a sharp drop ($t = 5.23$, d.f. = 5, $p = 0.0003$) across the clear-cut edges up to 20 m inside the forest (Fig. 2). The percent of exposed soil also changed more abruptly at clear-cut edges ($t = 2.24$, d.f. = 5, $p = 0.048$) than at wildfire edges. Shrub cover increased 20% in the first 20 m of the interior part of the clear-cut transects while it diminished gradually across the wildfire edges. These changes in shrub cover were marginally significant between the two types of edge ($t = 2.03$, d.f. = 5, $p = 0.069$) but responses were in opposite directions (Fig. 2). While we detected no significant difference in the abruptness of the change in canopy cover ($t = -0.96$, d.f. = 5, $p = 0.36$), there was no canopy cover in the clear-cut transects until the edge where it rose sharply. Thus, four habitat variables changed similarly across both types of edges and three environmental variables (CWD cover, exposed soil and shrub cover) changed more abruptly at the clear-cut edges than at burned edges. These changes support our first prediction that environmental variables are likely to have a sharper edge effect at clear-cut edges.

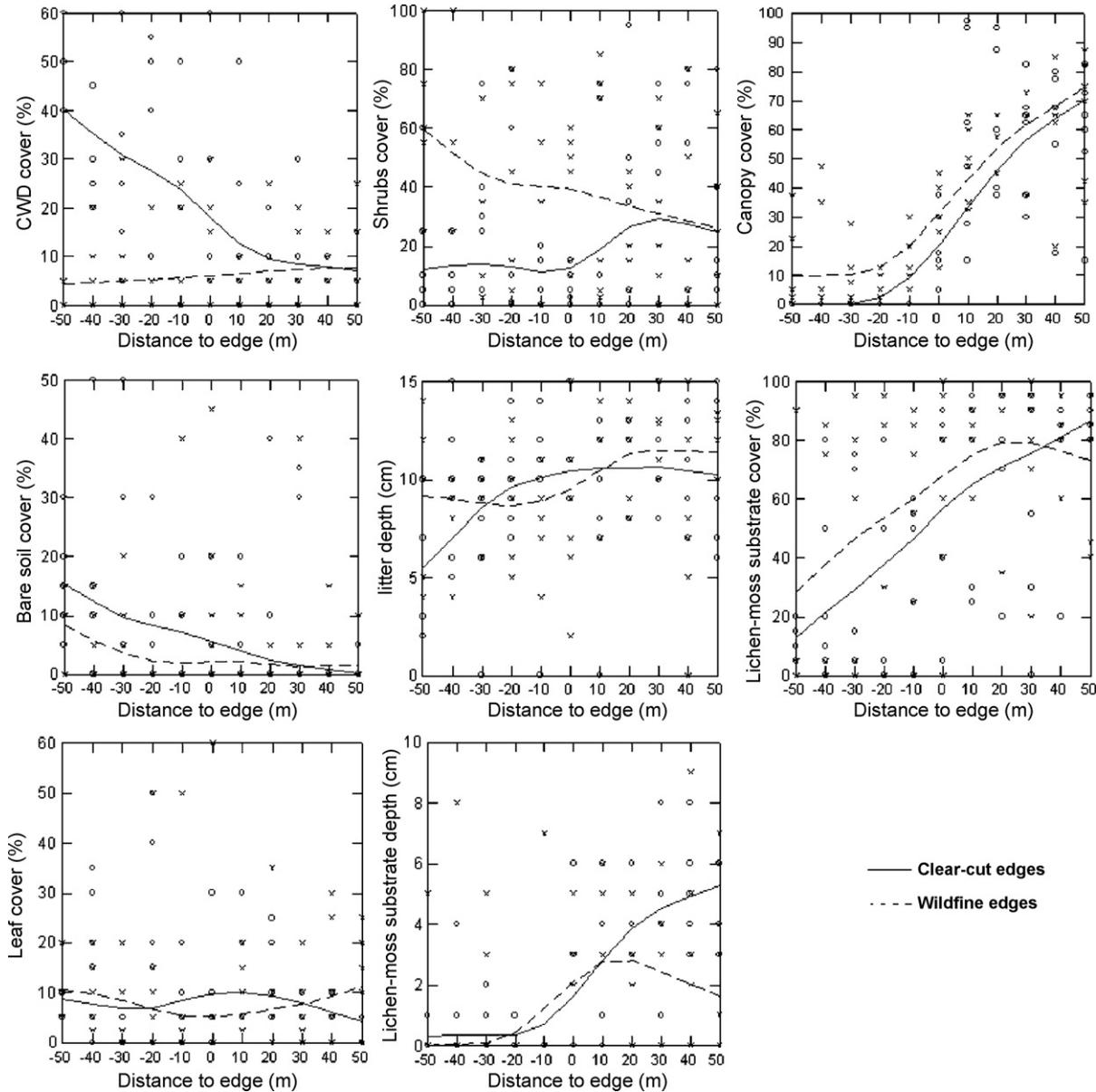


Fig. 2. Changes in the values of the forest floor and vegetation attributes measured along the edge transects, using the LOWESS (tension = 0.5) smoothing technique. Values on the x-axis correspond to the locations on the transects, with negative values indicating distances into the disturbance and positive values distances into the forest interior.

3.2. Spider assemblages' response to the edges

Spider assemblages' responses to edges are shown in Fig. 3a and b. The first axis of both CA's represents a distance gradient between assemblages found inside the disturbances with those found in the forest interior section of the transects. Notice the small size of the confidence ellipse of the clear-cut assemblages (spiders sampled between 20 and 50 m in the clear-cuts), which depicts low variability in the species composition of spider assemblages found from one site to another (Fig. 3a). In addition, the ellipse representing clear-cut assemblages is totally embedded within the edge ellipse indicating that the spider assemblages found in the clear-cut section of the transects were a subset of the assemblages found at the edges of the clear-cuts. The lack of overlap of the ellipse from the forest

interior of the clear-cut transects and the other two ellipses suggests that spider assemblages in the forest interior were distinct from those of clear-cut edges (Fig. 3a). The larger size of the forest interior ellipse also indicates that these assemblages were more variable than the assemblages at the edges.

For spider assemblages in wildfire-forest transects (Fig. 3b), there was a high overlap between spider assemblages found in the wildfire and those at the edge, whereas the overlap between the edge ellipse and the interior ellipse was smaller. Also, the position of the ellipses in the ordination plot shows a transition in the composition of spider assemblages from burned, to edge, to the interior section of the transects. Hence, the variation in species composition of spider assemblages is more gradual across the fire edges than across the clear-cut edges supporting

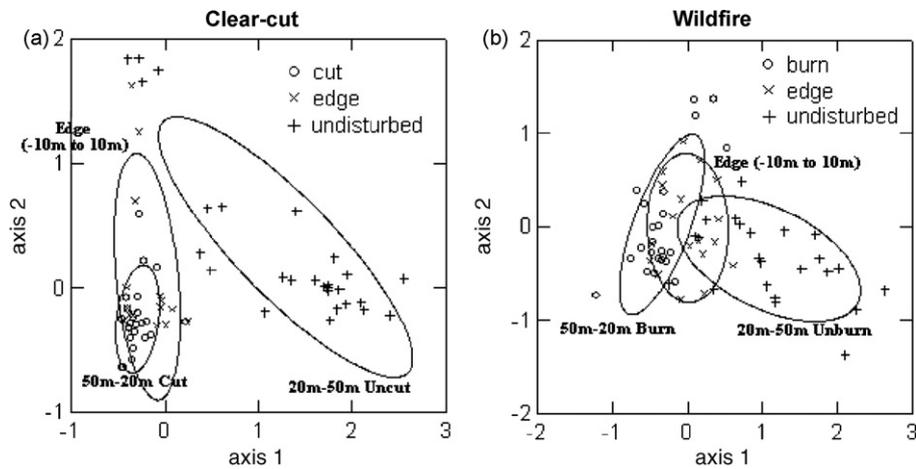


Fig. 3. (a) Ordination of the 66 traps of the six 100 m transects across clear-cut edges based on a correspondence analysis (CA) of spider species composition. (b) Ordination of the 66 traps of the six 100 m transects across wildfire edges based on a correspondence analysis (CA) of spider species composition. 67% concentration ellipses for the distance groups are shown.

our first prediction that clear-cut edge effects are sharper than the edge effects at burned edges.

The spider species that were most influential in the correspondence analyses are shown in Table 1. The first axis loadings of both CA's in Table 1a and b are associated with the gradients from disturbed habitat (negative loadings) to forest interior (positive loadings) seen in Fig. 3a and b. Spiders with negative loading values (disturbed part of CA's in Fig. 3a and b) in axis 1 of Table 1 are open habitat spiders and mostly lycosid species from the genus *Pardosa*. Those with positive loading values in Table 1 (forest interior part of CA's in Fig. 3a and b)

Table 1
Correspondence analysis loadings of the 10 spiders contributing most to the first two CA axes for the clear-cut and wildfire edge ordinations

	Loadings	
	AX1	AX2
(a) Clear-cut edges		
<i>Pardosa uintana</i> (Gerstch)	-0.4783	-0.4781
<i>Pardosa moesta</i> Banks	-0.6468	-0.9713
<i>Pardosa hyperborea</i> (Keyserling)	-0.4439	1.8514
<i>Pardosa xerampelina</i> (Keyserling)	-0.5762	-0.7033
<i>Cybaeopsis tibialis</i> (Emerton)	1.8713	0.3592
<i>Diplocentria bidentata</i> (Emerton)	1.0765	-0.1979
<i>Sisicottus montanus</i> (Emerton)	2.5466	-0.4333
<i>Pardosa mackenziana</i> (Hentz)	-0.4677	-0.4494
<i>Pocadicnemis americana</i> Millidge	-0.2764	2.4378
<i>Improphantes complicatus</i> (Emerton)	2.6092	-0.1248
(b) Wildfire edges		
<i>Pardosa hyperborea</i> (Thorell)	-0.4227	-0.5457
<i>Pardosa uintana</i> (Gerstch)	0.3617	1.8219
<i>Pardosa xerampelina</i> (Keyserling)	-0.7728	1.006
<i>Cybaeopsis tibialis</i> (Emerton)	2.25	-0.3057
<i>Alopecosa aculeata</i> (Clerck)	-0.4408	-0.1987
<i>Pardosa mackenziana</i> (Keyserling)	-0.2221	1.0506
<i>Pocadicnemis americana</i> Millidge	-0.0038	-0.6515
<i>Pardosa moesta</i> Banks	-1.8797	-0.897
<i>Walckenaeria tricornis</i> (Emerton)	1.568	-1.0243
<i>Diplocentria bidentata</i> (Emerton)	0.8938	-0.4138

are associated to mature interior habitat and are mostly sheet-web builders.

Correlations of environmental variables with the first axis of both ordinations were highest for percent canopy cover and the depth of the lichen-moss carpet. Litter depth was only correlated with the first axis of the wildfire edges ordination whereas the percent cover of the lichen-moss substrate was correlated only with the first axis of the clear-cut edges ordination (Table 2). The percent cover of coarse woody debris and of exposed soil were the strongest environmental correlates of the second axis of the clear-cut edges ordination whereas the percent cover of shrubs was the highest correlate for the second canonical axis of the wildfire edges ordination (Table 2).

Table 2
Correlations of the environmental variables with the first two axes of the canonical correspondence analysis performed on the spider species matrices (for clear-cut and wildfire edges) constrained by the environmental variables

	Wildfire edges		Clear-cut edges	
	AX1	AX2	AX1	AX2
Species-environment correlations	0.90	0.75	0.92	0.81
Environmental variables				
Lichen-moss depth	0.35	-0.04	0.51	-0.62
Litter depth	0.44	0.03	0.14	-0.18
Exposed soil	0.09	0.11	-0.24	0.39
Leaves% of cover	0.20	0.35	-0.10	0.28
Lichen-moss% of cover	0.12	-0.13	0.39	-0.60
Shrubs% of cover	-0.46	-0.46	0.18	-0.37
Woody debris	0.00	0.07	-0.41	0.45
% of canopy cover	0.83	-0.22	0.91	0.04

The first canonical axis ($p < 0.005$) and all the canonical axes ($p < 0.005$) were found to be significant using a Monte-Carlo permutation test. The correlation of each environmental variable indicates its contribution to the explained variance of the spider matrix by the environmental variable matrix. The first two axes of the wildfire transect's CCA explain 58.4% (AX1 40.6% and AX2 17.8%) of the variation between the spider and the environmental variable matrices while those of the clear-cut transect's CCA explain 68.0% (AX1 43.5% and AX2 24.5%).

Table 3
Indicator value (%) for ground-dwelling spiders in the three edge zones: open (disturbed) area (–50 m to –20 m), edge (–10 m to 10 m) and forest interior (20–50 m)

Species	Indicator value				p-Value
	Cut	Edge	Interior	Overall	
Species characteristic of 2-year-old clear-cuts					
<i>Pardosa moesta</i> Banks	83	10	0	83.4	0.001
<i>Pardosa uintana</i> (Gerstch)	52	37	2	52.1	0.001
<i>Pardosa xerampelina</i> (Keyserling)	67	16	0	66.9	0.001
<i>Trochosa terricola</i> Thorell	28	6	2	27.7	0.027
Species characteristic of 2-year-old clear-cut edges					
<i>Pardosa mackenziana</i> (Keyserling)	31	33	0	32.8	0.051 ^a
Species characteristic of mature forest interior					
<i>Cybaeopsis tibialis</i> (Emerton)	7	23	48	48.4	0.002
<i>Improphantes complicatus</i> (Emerton)	3	9	41	40.6	0.006
Species characteristic of 2-year-old wildfire					
<i>Alopecosa aculeata</i> (Clerck)	50	16	7	50	0.001
<i>Micaria aenae</i> Thorell	25	0	0	25	0.008
<i>Pardosa hyperborea</i> (Thorell)	44	40	9	43.9	0.028
<i>Pardosa moesta</i> Banks	27	7	0	27.2	0.054 ^a
<i>Pardosa xerampelina</i> (Keyserling)	47	20	0	46.5	0.001
<i>Neoantistea agilis</i> (Keyserling)	39	13	0	38.5	0.002
Species characteristic of 2-year-old wildfire edges					
<i>Pardosa mackenziana</i> (Keyserling)	26	41	1	40.9	0.017
Species characteristic of mature forest interior					
<i>Cybaeopsis tibialis</i> (Emerton)	4	12	56	55.9	0.001
<i>Robertus fuscus</i> (Emerton)	1	0	25	25	0.007
<i>Walckenaeria directa</i> (O.P.C.)	0	7	43	42.9	0.001

^a Species with *p* values near 0.05 are included in the table due to the low statistical power of the permutation test to reduce the rate of Type II error.

3.3. Guild responses across edges

The species indicator analysis identified eight spider species as open habitat spiders (both disturbances combined) whereas five species were categorized as interior habitat species and only one species, *Pardosa mackenziana* (Keyserling), was significantly associated with both the burned and the clear-cut edge zones (Table 3). Open habitat specialists decreased in abundance at the beginning of the edge transects inside the clear-cuts and the burned habitat up to 30 m inside the forest interior at the clear-cut transects and 50 m inside the forest interior at the wildfire transects (Fig. 4). The regression slopes were significantly more negative, i.e., more abrupt, for the clear-cut edges than wildfire edges ($t = 6.99$, d.f. = 5, $p = 0.001$). Forest interior specialists dropped in abundance from 30 m inside the forest interior to 50 m inside the clear-cuts and from the 50 m inside the forest interior (the end of our transects) to 20 m inside the recently burned habitat (Fig. 4). There was no difference in abruptness of this change between the clear-cut and wildfire transects ($t = 0.86$, d.f. = 5, $p = 0.429$). Open habitat species richness changed more abruptly in clear-cut edge transects than wildfire one ($t = 3.64$, d.f. = 5, $p = 0.015$). Open habitat species richness dropped abruptly between 10 m inside the clear-cuts to 30 m inside the forest interior part of the transects while it dropped between 20 m inside the burned habitat until 40 m inside the forest interior along the burned edges (Fig. 5). The change in richness of interior habitat spiders was not significantly

different ($t = 1.21$, d.f. = 5, $p = 0.28$) between the two types of edges (Fig. 5). Thus, the abundance and the richness of open habitat spiders changed more abruptly at the clear-cut edges than the wildfire edges. These results agree with our predictions as the changes in abundance and richness at clear-cut edges were more abrupt but our results do not indicate that clear-cut edges have a shorter DEI than wildfire edges.

4. Discussion

4.1. Response of environmental variables to edges

The more abrupt change in the percent cover of coarse woody debris, exposed soil and shrub cover at the clear-cut edges than the wildfire edges supports our first prediction that environmental variables along edges resulting from clear-cuts change more abruptly than along edges of wildfire (Forman, 1995; Voller and Harrison, 1998; Harper et al., 2005). Similarly, Harper et al. (2004) found more abrupt changes in CWD, lichen diversity, and overall habitat structure at recent clear-cut edges compared recently burned edges concluding that recent wildfire edge effects were wider for vegetation and habitat structure. CWD and exposed soil are environmental variables part of the primary response to newly created edge while shrub cover is part of the secondary response. The primary response variables are involved in the initial changes in vegetation, habitat structure and microclimate due to the disturbance while the secondary response variables involve change in understory

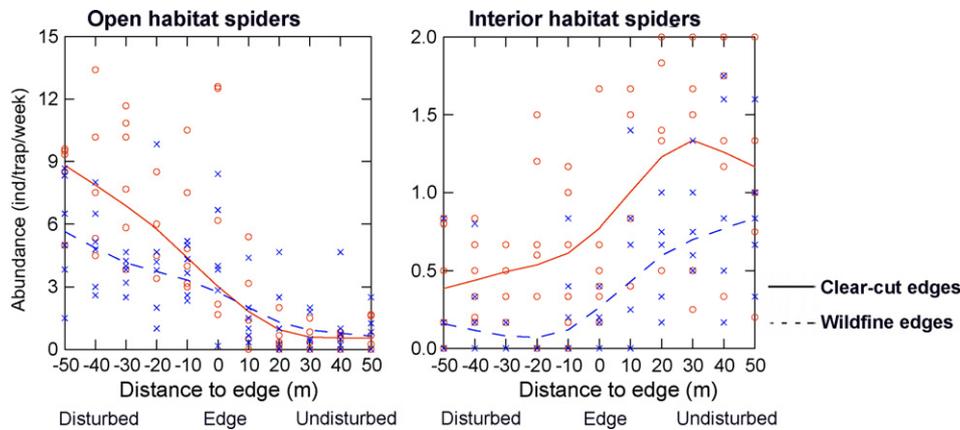


Fig. 4. Distribution of the open- and interior-habitat species abundance across the clear-cut-forest and wildfire-forest edge transects. The LOWESS (tension = 0.5) smoothing techniques fits the pooled abundance (number/trap/week) of each group of species across the transects. Values on the x -axis correspond to the locations on the transects.

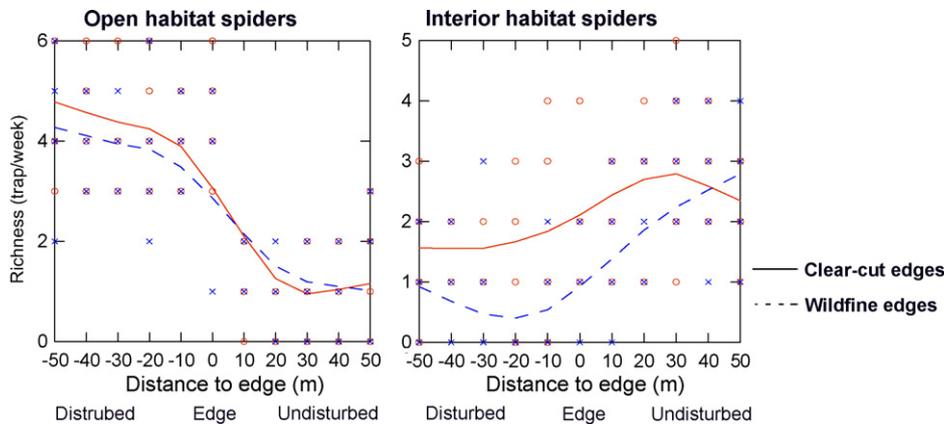


Fig. 5. Distribution of the open and interior-habitat species richness across the clear-cut-forest and wildfire-forest edge transects. The LOWESS (tension = 0.5) smoothing techniques fits the richness (number of species/trap/week) of each group of species across the transects. Values on the x -axis correspond to the locations on the transects.

structure and species composition (Harper and Macdonald, 2002). The secondary response can arise from microclimatic changes and also from changes in the primary response variables. This could explain why we observed significant changes in CWD and exposed soil percentages across our edge transects as they are part of the primary response. Other variables such as the lichen–moss substrate cover and depth are secondary response variables to recently created edges. Changes in the cover percentage of these variables result from direct effects of edges on the microclimate and the primary response variables. The secondary response generally lags behind the primary response (Matlack, 1993; Harper and Macdonald, 2002) as it is influenced by the primary response variables, this could explain why we did not detect a change in abruptness in our variables associated with this type of response. We detected a more abrupt change at clear-cut edges also in shrub cover even though it is identified as a secondary response variable. Dominant shrubs associated with the forest floor of boreal forests such as *Vaccinium sp.* and *L. groenlandicum* have deep root systems that allow them survive intense fires. As such they rapidly occupy the shrub cover after wildfires. Also, wildfires of high severity (index of 5 out of 5)

such as the one in the park create fire edges that are more abrupt than wildfires with a lower severity index would. Therefore, the edges created by the Parc des Grands Jardins fire are potentially closer to clear-cut edges than edges arising from wildfires with lower fire severity.

Our results nevertheless show that the species composition of spider assemblages changes gradually across recent wildfire and clear-cut edges but a more abrupt shift occurs in the spider assemblages at clear-cut than at fire edges. The ellipses representing each edge zone on the CA ordination of the clear-cut transects did not overlap with one another while those of the CA ordination from the wildfire transects did show some overlap indicating a more gradual change in the composition of the spider assemblages along our wildfire edge transects. Also, open habitat spiders showed a significantly more abrupt response in their abundance and richness to the clear-cut edges than wildfire edges. Therefore, the more abrupt changes in composition of the spider assemblages and of open habitat spider's abundance and richness across clear-cut edges than wildfire edges provide support for our first prediction. Spiders have a well documented history of responding primarily to habitat structure and conditions (Wise, 1993; Buddle et al., 2000; Larrivé et al.,

2005). These results suggest that spiders are sensitive to differences between clear-cut and wildfire edges as we were able to document similar patterns of change across wildfire and clear-cut resulting from edge effects both in habitat structure variables and in the spider assemblages. Yu et al. (2007) document an edge Carabidae fauna more similar to the interior forest Carabidae fauna in a study dealing with hard edges at the interface between grasslands and deciduous forests in southwestern China.

We did not find that spider assemblages were more abundant or rich at the edge zone of both types of disturbances. This pattern was documented in other studies where some arthropod groups were significantly more abundant or richer at the edges compared to inside the two habitats adjacent to the edge (Helle and Muona, 1985; Jokimaki et al., 1998; Magura et al., 2001; Molnár et al., 2001; Magura, 2002; Pearce et al., 2005; Mathe, 2006; but see Taboada et al., 2004 for similar assemblage response to this study). Such species or group of species were labelled as edge specialists in these studies. Pearce et al. (2005) identified eight ground-dwelling spider species associated with 5–10 years old clear-cut edges. Jennings et al. (1988) also record *Diplocentria bidentata* (Emerton) more abundantly at clear-cut edges than the forest interior. This species, commonly detected in our study was labelled as a generalist species as it did not show any association to a particular edge zone in our species indicator analysis. In our study, only one species, *P. mackenziana*, was significantly associated with edge habitats in our species indicator analysis. The very recent creation of the edges in our study (2 years) compared to the edges in Pearce et al. (2005) and Jennings et al. (1988) could explain why we only detected one edge specialist species. Even though we detected only one edge specialist, the potential for edge specialist species in boreal forests is there as the high frequency and recurrence of wildfires and windthrows (Bergeron et al., 1999; Buddle et al., 2006) contributed to the creation of many edges in boreal forests since the last glaciations. Edge specialist species have potentially arisen by benefiting from the historical availability of edge habitat generated by wildfires. As such, the presence of edge specialists in the fauna of ground-dwelling spiders associated with the boreal forest floor is possible as the ground-dwelling fauna has been exposed to edge conditions over a significant time scale. The classification of *P. mackenziana* in our study and of other ground-dwelling spiders in Pearce et al. (2005) and Jennings et al. (1988) as specialists of clear-cut edges could be explained by the fact that some boreal forest wildfire edges originating from severe fires are as sharp as clear-cut edges. On the other hand, studies on ground-dwelling beetles (Carabidae) and edge effects (Spence et al., 1996; Heliola et al., 2001; Pearce et al., 2005) did not find any edge specialists perhaps because none have evolved in this beetle family or because the type of wildfire edges generally created in their study areas does not reflect the abrupt edges created by logging (Baker et al., 2007). This demonstrates that more comparative research on the edge effects of clear-cuts and wildfires of different ages at varying severity is needed as the response of ground-dwelling arthropods to logging edges may be tightly linked to the type of edges arising from this disturbance regime where the logging occurs.

4.2. Extent of edge influence

The response we obtained both for the abundance and richness of open and interior forest specialists through our LOWESS smoothing procedure corresponds to the transitional response of the edge effect model developed by Ries and Sisk (2004) when the edge is between two very different habitats. They associated this type of response with either edge avoidance as the species avoid the environmental changes occurring at the edge as they are hostile to them or with high resource concentration in the typical habitat for the modelled organisms and low resource concentration across the edge into the lower quality habitat. These transitional changes in abundance apply to both open and interior specialist species living on both sides of the edges.

The distance of edge influence (DEI) of wildfire and clear-cut edges on the abundance of open habitat specialist ground-dwelling spiders extended to the limit of our transects inside both disturbances while it levelled off at 30 m inside the forest interior. This shorter DEI on open habitat specialist abundance and richness inside the forest interior across our clear-cut edge transects supports our second prediction that clear-cut edges have a shorter DEI. This can be related to the significantly more abrupt changes in abundance and richness of open habitat spiders across our clear-cut transects. The abundance and richness of forest interior specialists consistently declined from the end of our transects at burned edges and started dropping 30 m inside the forest interior at clear-cut edges. Forest interior specialists had basically disappeared 20 m inside the wildfire transects and levelled off at 30 m inside the clear-cuts. These various DEI's are reflected by changes in the spider assemblages across the edge transects by drops in abundance, as only certain individuals can withstand the new conditions, and richness, as some populations simply disappear until there is no more edge effect inside their habitat. Such changes in numbers can occur between wildfire and clear-cut edge transects since ground-dwelling spiders associated with interior forests mostly do not survive severe wildfires and are seldom collected recently after such fires. On the other hand, recent clear-cuts are known to harbour residuals populations of ground-dwelling forest interior species (Huhta, 1971; Buddle et al., 2000; Larrivéé et al., 2005). The same phenomenon is documented in Carabidae (Spence et al., 1996; Saint-Germain et al., 2005). This could explain the higher abundance and richness of interior forest specialists inside the clear-cut section of our edge transects. The presence of interior specialist species inside the disturbed part of the edges could suggest the edges are acting as population sinks (Didham, 1998) but it would be premature to come to such conclusion in our study since edges were recently created (2 years old). As such, changes documented in our study reflect mostly the effects of changes in habitat structure and vegetation composition (Harper and MacDonald, 2001). These changes render the cover type within the DEI more or less suitable depending on which cover type the species are associated with. Therefore, our interpretations are based on changes in population numbers due to the newly created conditions.

The DEI distances are consistent with our results for the environmental variables and with most previous work on the responses of plants and animals to edges (Matlack, 1993; Murcia, 1995; Baker et al., 2007; but see Spence et al., 1996 for up to 80 m). Thus, the total DEI, as defined by the sum of the DEI on each side of the edge on ground-dwelling spiders, was approximately 60 m wide for both disturbances in our study.

Although it is recognized that edge effects occur on both sides of the adjacent cover types (Forman, 1995; Baker et al., 2002), most studies measuring the extent of edge influences focus on the forest interior. However, the forest interior has been shown to exert an influence on the disturbed cover type by affecting abiotic factors (lower air and soil temperatures, wind, irradiance and higher moisture) to distances of up to 20 m (Cadenasso et al., 1997; Davies-Colley et al., 2000; Magura, 2002). This could explain why a reduction in abundance of open habitat spiders begins around 30 m inside the disturbed part of the edges and why the interior habitat spiders only reach their expected low abundances inside the disturbed habitats at around the same distance of 30 m inside the clear-cut and wildfire transects.

5. Management considerations and conclusions

Edges have always been a part of boreal ecosystems as recurrent wildfires that create edges between burned areas and unburned areas have been the most important disturbance in boreal ecosystems for millennia (Niemela, 1999; Bergeron et al., 1999, 2002, 2004; Harper et al., 2004). Our results show that both the clear-cuts and the wildfire produced edge effects on ground living spider assemblages. We found evidence in support of our prediction that clear-cut edges are more abrupt and therefore have a shorter DEI on the forest interior than wildfire edges. However, one of the most important characteristics that distinguish forest harvesting from wildfires is the varying severity of wildfires (Kafka et al., 2001; Bergeron et al., 2002). Therefore, before extrapolating our findings, more research incorporating a comparative design such as ours, should be conducted along edges that encompass a gradient of fire severity.

The impact on biodiversity created by the loss of naturally created wildfire edges is of concern in the black spruce boreal forest landscape. Over a longer time scale, recent cut edges may not be able to emulate completely those of recent wildfires creating a gap in recent wildfire edges habitat availability. Thus, forest management strategies such as “feathered” edges or partial cuts near the edges added to the current practices could help alleviate the differences between recent cut and wildfire edges (Harper et al., 2004). Other differences between the two edge types such as the increased amount of CWD at wildfire edges documented in this study and by Harper et al. (2004) may not be emulated by management practices and are important features for wildlife (Varady-Szabo and Buddle, 2006).

In our study, the more gradual change in spider assemblages at the wildfire-forest edge suggests that planning of less sharp edges in timber harvested is likely to increase the similarity between spider assemblages at the edges of these newly

designed clear-cuts and those of wildfire edges. Planning clear-cuts with a more sinuous shape, with partial retention of live stems, with less woody debris and exposed soil within a 30 m buffer at the remnant forest–cutover area interface could reproduce partly the conditions of partial burning often observed in wildfires (Harper et al., 2004; Bergeron et al., 2004). Understanding the functional role of this structural complexity on spider assemblages at fire edges will require more research on the underlying processes that are related to the patterns documented in this paper.

The 60 m wide DEI created by wildfires and clear-cuts provides relevant information for determining the minimum width of forest remnants, riparian or road buffers, and forest strips between cut-blocks to maintain forest interior species. We suggest that a minimum width of 100 m is necessary for such remnants to retain any forest interior spider assemblages. While this could differ for other taxa, the edge avoidance patterns of the forest interior specialists documented here seem to reflect the responses of most interior habitat species of ground-dwelling arthropods investigated in boreal forests subjected to similar logging regimes (Buddle et al., 2000; Saint-Germain et al., 2005; Larrivée et al., 2005). In a study conducted in black spruce managed landscapes of northwestern Québec, Lopez et al. (2006) also suggest that linear remnant habitats less than 60 m do not offer adequate forest interior conditions while being strongly exposed to edge influence. Boudreault et al. (2008) also found that epiphytic lichens are unlikely to persist in linear remnants less than 60 m and discuss the importance of having a more gradual transition of structural elements at clear-cut edges to reduce edge effects for epiphytic lichens that persist in remnant forests in managed landscapes.

Finally, this study was conducted 2 years following the wildfire and timber harvesting disturbances. Previous studies have shown that edge effects are dynamic through time and will tend to diminish with time since the creation of the edge (Matlack, 1993; Harper and Macdonald, 2002; Ries et al., 2004). Therefore, further comparisons on the edge effects of wildfires and clear-cuts at various times since edge creation of the edges could refine our interpretation of the differences or similarities that these two types of disturbance may have on edge effects issues.

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