Effects of experimental harvesting on spider (Araneae) assemblages in boreal deciduous forests[1]

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Abstract—Two large-scale forestry experiments, in Quebec (Sylviculture et aménagement forestiers écosystémique (SAFE)) and Alberta (Ecosystem Management by Emulating Natural Disturbance (EMEND)), were established in the late 1990s to test the effects of alternative silvicultural strategies (*e.g.*, partial cutting) on biodiversity in northern boreal forests. We collected spiders in pitfall traps 2 years after the application of partial-cutting treatments in deciduous stands at EMEND and 6 years after similar treatments in deciduous stands at SAFE. Although we are aware of the challenges imposed by disparate locations and whole-scale experimental methods, our objective was to compare the effects of partial cutting on spider assemblages (diversity and community composition), and in doing so, to formulate a few general statements. Overall, 98 species (6107 individuals) were collected from Alberta and 86 species (3414 individuals) from Quebec. Of these, 44 species were common to both regions. Ordination and indicator-species analyses revealed a distinct effect of geographic separation: the spider assemblages in deciduous stands within the boreal plains ecoregion of Alberta and the boreal shield in Quebec were distinct. However, the effects of partial cutting on spider assemblages within each project were similar: removal of 25%–33% of trees shifted a characteristic old-growth fauna toward one more typical of clearcuts. Indicator-species analysis also revealed the dominance of wolf spider (Lycosidae) species in clearcuts within both experiments and we present evidence that clear-cutting homogenizes spider assemblages. Old-growth forests contain spider faunas that are easily disrupted by moderate partial cutting. In the face of intense harvesting practices, managing for the maintenance of biodiversity and conservation of spider faunas in northern forests will require retention of old-growth forests.

Résumé—Deux expériences forestières à grande échelle, au Québec (Sylviculture et aménagement forestier écosystémiques (SAFE)) et en Alberta (Ecosystem Management by Emulating Natural Disturbance (EMEND)), mises en branle à la fin des années 1990 cherchent à vérifier les effets de pratiques de sylviculture de rechange (c'est-à-dire, des coupes partielles) sur la biodiversité des forêts boréales nordiques. Nous avons récolté des araignées dans des pièges à fosse 2 ans après un traitement par coupe partielle dans des peuplements décidus dans le cadre d'EMEND et 6 ans après un traitement semblable dans des peuplements décidus dans le cadre de SAFE. Tout en étant conscients des problèmes générés par ces sites disparates et des méthodes expérimentales à grande échelle, notre objectif est de comparer les effets de la coupe partielle sur les communautés d'araignées (diversité et composition) et, par là, arriver à quelques conclusions générales. Globalement, nous avons récolté 98 espèces (6107 individus) en Alberta et 86 espèces (3414 individus) au Québec; de celles-ci, 44 espèces sont communes aux deux régions. Des ordinations et des analyses d'espèces indicatrices indiquent un net effet de la distance géographique : les communautés d'araignées des peuplements décidus dans l'écorégion des plaines boréales de l'Alberta et dans le bouclier laurentien boréal du Québec sont distinctes. Cependant, les effets de

Received 20 May 2006. Accepted 14 April 2007.

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

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https://doi.org/10.4039/n07-LS01 Published online by Cambridge University Press

la coupe partielle sur les communautés d'araignées dans chacun des deux projets sont semblables : un retrait de 25 % – 33 % des arbres entraîne un remplacement de la faune typique des forêts anciennes par une faune plus caractéristique des zones de coupe à blanc. L'analyse des espèces indicatrices montre aussi une dominance des espèces d'araignées-loups (Lycosidae) dans les zones de coupe à blanc dans les deux expériences; nous présentons des preuves que la coupe à blanc tend à homogénéiser les communautés d'araignées. Les forêts anciennes contiennent des faunes d'araignées qui sont facilement perturbées par une coupe partielle modérée. Lors de l'utilization de méthodes de coupe à forte intensité, il sera nécessaire de préserver des forêts anciennes pour permettre un aménagement qui favorise le maintien de la diversité et la conservation des faunes d'araignées.

[Traduit par la Rédaction]

Introduction

Boreal forestry practices should be based on natural forest dynamics, with explicit use of historical disturbance regimes as a guide for management (*e.g.*, wildfire, insect outbreaks, windthrow) (Hunter 1993; Haila *et al.* 1994; Angelstam 1998; Spence and Volney 1999; Spence *et al.* 1999; Bergeron *et al.* 2002). In general, even-aged stand management is unlikely to meet this goal, and thus other approaches such as partial cutting and variable retention should be combined with (or replace) traditional clear-cutting. Such adaptive management strategies may yield stand structure and cover types that are more closely aligned with natural forest dynamics. However, direct tests of this hypothesis require experimentation on the land base, using well-replicated designs with spatial and temporal controls. Additionally, such tests are required for a broad range of forest processes, flora, and fauna, and from different geographic regions.

Intensified forestry activities remain a key threat to biodiversity conservation (Vitousek *et al.* 1997; Simberloff 1999; Larsson and Danell 2001), and in northern forests, this is often caused by increased forest fragmentation and habitat loss. Conservation of biodiversity in these systems is a key priority. One of the many indicators that will inform stakeholders about the success of alternative silvicultural strategies is their effects on overall forest biodiversity. When selecting indicator groups for such work, ground-dwelling spiders (Araneae) represent a model taxon.

Spiders are one of the dominant ground-dwelling arthropod taxa occurring in temperate and northern forest ecosystems (Niemelä *et al.* 1996; Work *et al.* 2004; Buddle *et al.* 2006). This group is well known taxonomically (Coddington and Levi 1991), has repeatedly been cited as important to detritus-based food webs in forest ecosystems (*e.g.*, Moulder and Reichle 1972; Lawrence and Wise 2004), occupies a wide breadth of habitats (Turnbull 1973), and has well-understood life-history characteristics (Wise 1993). For these reasons, ground-dwelling spider assemblages are often used as ecological indicators (McGeoch 1998) in research relating to the conservation of biodiversity in human-disturbed landscapes, including boreal forests of Fennoscandia (Huhta 1971; Pajunen *et al.* 1995; Niemelä *et al.* 1996) and Canada (Buddle *et al.* 2000; Pearce *et al.* 2004; Work *et al.* 2004; Larrivée *et al.* 2005; Buddle *et al.* 2006), and other temperate forests in the United States of America (Coyle 1981; Jennings *et al.* 1988; McIver *et al.* 1992).

There is a good literature base for documenting patterns of spider diversity and community composition in temperate and northern forest ecosystems. For example, Pearce *et al.* (2004) showed that spider communities vary according to overall tree species composition: distinct faunas were associated with coniferous *versus* deciduous boreal forest cover classes. Work *et al.* (2004) found more diffuse effects when comparing cover classes, but this may have been due to low sample sizes. Research in parts of North America and Fennoscandia has documented the response of spiders to forest clearing. In general, cutover areas (and forest edges) are dominated by diurnal hunting spiders (*i.e.*, those not using webs to capture prey, including such families as Lycosidae (wolf spiders)), whereas mature forests tend to be characterized by web-building species, most notably of the families Amaurobiidae (in North America) and Linyphiidae (Huhta 1971; McIver *et al.* 1992; Pajunen *et al.* 1995; Buddle *et al.* 2000; Pearce *et al.* 2004). Diversity of spiders is sometimes elevated in recent clearcuts (Jennings *et al.* 1988; Pajunen *et al.* 1995), owing perhaps to faunal mixing (*i.e.*, open-habitat species, generalists, and relicts of closed-canopy forests). There are

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some contradictory reports on the effects of recent clear-cutting on spider assemblages. Larrivée *et al.* (2005) showed that clearcuts homogenize the spider fauna, whereas Buddle *et al*. (2000, 2006) showed the opposite effect.

There have also been various faunistic studies of spiders in boreal regions (Koponen 1995; Aitchison and Sutherland 2000), and some work has specifically included the short-term (Koponen 1993; Aitchison-Benell 1994; Koponen 2005; Larrivée *et al.* 2005) and long-term effects (Huhta 1971; Buddle *et al.* 2000) of wildfire on spider assemblages. Key findings from this work illustrate that wildfire creates unique habitats. Consequently a distinct fauna is associated with pyrogenic stands and this can promote variability in spider assemblages (Buddle *et al.* 2000). Chronosequence studies have also been used to compare spider assemblages in wildfire and clearcut-origin stands: faunal succession occurred more rapidly following harvesting than after wildfire (Buddle *et al.* 2000, 2006).

Still, some important questions remain about the effects of forestry activities on spider assemblages in northern forest ecosystems. In particular, very little quantitative information is available about whether forest-harvesting effects depend on regional differences in the fauna. In North American boreal forests, there is also scant information about the effects of alternative harvesting methods on spider assemblages (but see Jennings *et al.* 1988). For example, we cannot adequately answer the question of whether threshold amounts of cover are required to maintain aspects of the spider fauna present in natural stands. We also have little direct information about which species or guilds may be most threatened by harvesting practices, and whether generalities exist between different boreal-forest regions.

We attempted to address these unknowns and report on the response of spider assemblages to alternative harvesting methods using two large-scale forestry experiments: Ecosystem Management by Emulating Natural Disturbance (EMEND) in Alberta (within the boreal-plains ecoregion) and Sylviculture et aménagement forestiers écosystémique (SAFE) in Quebec (within the boreal-shield ecoregion). We have selected representative samples from the data gathered from these experiments in order to compare the effects of various partial-cutting treatments on spider assemblages. More detailed experiment-specific results will be published elsewhere. Specifically, we have addressed the relative short-term effects (2–6 years post treatment) of these experimental silvicultural treatments on spiders from deciduous-dominated cover types. Data from each region have been integrated directly, and we can therefore compare regional and local effects on all species from both experiments, as well as on species common to both regions. Our objectives were to determine (*i*) regional differences in spider assemblages between deciduous forests in the boreal-plains ecoregion (Alberta) and the boreal shield (Quebec) ecoregion, (*ii*) the effects of partial cutting (as exemplified by the two large-scale forestry experiments) on the diversity, abundance, and community composition of ground-spider assemblages, (*iii*) the differences between these effects in the two ecoregions, and (*iv*) whether any spider species or guilds are particularly sensitive to forestry activities.

Methods

Experiment descriptions and design

The EMEND experiment is situated in the Clear Hills Upland, Lower Foothills Ecoregion of Alberta, approximately 90 km northwest of Peace River (experiment centre 56°46′13″N, 118°22′28″W). Mixedwood stands range in age from 80 to 140 years and are dominated by trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*P. balsamifera* L.) (Salicaceae), and white spruce (*Picea glauca* (Moench) Voss) (Pinaceae). This large-scale, interdisciplinary experiment was defined in 1997 with two overall objectives: (1) to determine the forest-harvest and regenerative practices that best maintain biotic communities in comparison with mixedwood landscapes that have originated through wildfire and other natural disturbance and (2) to evaluate these harvesting practices in terms of social acceptability, economic viability, and sustainability. A 1000 ha area was partitioned on the basis of canopy composition before harvest following the typical post-disturbance successional trajectory of aspen-dominated to conifer-dominated cover types. Three 10 ha compartments of each cover type were harvested during winter 1998, leaving one of five proportions of residual material: (1) 0%–2% (clearcut), (2) 10%, (3) 20%, (4) 50%, and (5) 75% (Spence and Volney 1999; Work *et al.* 2004). These proportions were obtained through a modified two-pass uniform shelterwood method. Each harvested compartment (with the exception of clearcut compartments) was completed with 5 m wide machine

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corridors and intervening 15 m wide and variously thinned retention strips. Treatment effects are interpreted in relation to two types of control, uncut compartments and experimentally burned compartments, each replicated spatially with the harvested compartments. Response variables to these cover types and harvest treatments include site productivity, succession and dynamics of biodiversity, hydrological processes, and soil nutrient dynamics. Experiment-wide richness and abundance of epigaeic invertebrates were assessed using pitfall traps in permanent collection plots prior to harvest (Work *et al.* 2004) and in the first, second, fourth, and fifth growing seasons post harvest. To best compare cover type and treatment effects on spider diversity with those observed in the SAFE experiment, we only used collections from aspen-dominated compartments during the second growing season and excluded experimentally burned compartments.

Pitfall-trapping for epigaeic invertebrates commenced 5–8 May 2000, one summer post harvest. We placed six pitfall traps in each compartment (n = 150, 1 cover type × 3 replicates × 6 treatments (unharvested controls had a total of 42 pitfall traps) × 6 pitfall traps). Traps were placed no less than 10 m apart and were paired in three permanent plots. With the exception of clearcut and control compartments, members of the trap pair were placed either in the middle of a machine corridor or in a retention strip. Pitfall traps were transparent plastic containers (11 cm diameter × 15 cm depth) containing an outer permanent cup and an inner sampling cup and covered with a square wooden roof (10 cm × 10 cm) held 3–4 cm above the trap by two nails. Propylene glycol, to a depth of 2–3 cm, was used as a preservative. Traps were serviced 5 times throughout the summer and removed between 19 and 24 August. Sampling periods averaged 105 trap-days; adult spiders were identified to species for all sampling periods.

The SAFE experiment is situated in the Abitibi region of northwestern Quebec, within the Lake Duparquet Research and Teaching Forest (approximately 48°86′–48°32′N, 79°19′–79°30′W). SAFE consists of several phases, each representing a different combination of silvicultural treatments and cover types. The data presented here are from phase 1, represented by even-aged, first-cohort trembling aspen forest. Forest age was 90–100 years prior to treatment establishment. During the winter of 1998–1999 the following treatments were applied to the land base: control (no harvesting), 2/3 partial cut (61% of merchantable stems manually harvested), 1/3 partial cut (33% of merchantable stems manually harvested), and clearcut (Brais *et al.* 2004). Each treatment was replicated in three blocks and randomly assigned to 1–2.5 ha compartments within each block. Additionally, controlled burns were completed during August 1999, but these treatments are not included here. Five permanent sampling plots were established within each compartment; each plot was circular, with a radius of approximately 11.28 m. These plots were used for subsequent vegetation monitoring and soil sampling (*e.g.*, see Brais *et al.* 2004).

Pitfall trapping for arthropods commenced 10–14 May 2004, 6 years post treatment. We placed 10 pitfall traps within each compartment (n = 120; 3 replicates (blocks) × 4 treatments × 10 pitfall traps); 2 traps were placed within each sampling plot (five plots per compartment); traps were about 5 m apart on opposite sides of the centre of the sampling plot. Pitfall traps were identical with those used in the EMEND experiment except that they were slightly smaller (7 cm diameter × 9.5 cm depth) and the elevated roof was a round plastic plate (10 cm radius); the size difference likely has little effect on spider catch rates (Work *et al.* 2002). Traps were serviced 6 times throughout the summer and removed on 26 August. Owing to logistical and time constraints, species-level identifications of adult spiders were completed for only three sampling periods encompassing a total of 47 trap-days: 29 May – 9 June, 10–26 June, and 9–26 August. These sampling periods were selected because they represent peak activity periods for many species occurring in boreal forests (Niemelä *et al.* 1994; Buddle and Draney 2004).

Species identifications and data management

Adult spiders were identified to species using various keys (*e.g.*, Dondale and Redner 1978, 1990; Paquin and Dupérré 2003). Voucher specimens have been deposited in the Lyman Entomological Museum (Sainte-Anne-de-Bellevue) for Quebec spiders and the Strickland Entomological Museum (Edmonton) for Alberta spiders.

Identification records were filtered through a nomenclator associated with the Nearctic Spider Database (Shorthouse 2007) to ensure consistent use of names across experiments, then stored in

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Table 1. Summary of species richness and catch rates (raw totals) for spider guilds collected in pitfall traps placed in EMEND and SAFE.

Guild*	Species richness	Catch rate
Ambushers (Philodromidae, Thomisidae)	16	534
Foliage runners (Clubionidae, Liocranidae)	4	279
Ground runners (Lycosidae, Gnaphosidae)	27	5177
Sheet-web builders (Agelenidae, Amaurobiidae)	13	1801
Space-web builders (Dictynidae, Theridiidae)	8	73
Stalkers (Salticidae)	5	11
Wandering sheet/tangle weavers (Linyphiidae)	66	1646
Total	139	9521

*Sample families are in parentheses. Guild classifications are adapted from Uetz *et al.* (1999).

a relational database in preparation for analyses. Data were pooled and standardized by total trap-days to accommodate variation in sampling effort between experiments and trap disturbances within experiments; consequently, catch rate (number of individuals per trap-day) was the sampling unit. Species were grouped by their guild membership as documented by Uetz *et al.* (1999) (Table 1).

Data analyses

Overall catch rates were used to compare spider faunas obtained from EMEND and SAFE to best control for the effects of trap disturbance and sampling intensity. We used a simple one-factor ANOVA (*i.e.*, with harvesting intensity as the main factor) to compare overall catch rates for each experiment separately. Diversity data were compared using individual-based rarefaction analysis to avoid the problems of using single-index diversity indices or raw species richness (Gotelli and Colwell 2001; Buddle *et al.* 2005). This approach allows for unbiased comparisons of species richness after accounting for variation in sampling effort. The software program Ecosim (Gotelli and Entsminger 2006) was used to compute rarefaction curves. To directly compare treatment types by experiment, we restricted the rarefaction comparisons to control plots, clearcut blocks, and two levels of partial cutting: 67%–75% residual material (*i.e.*, 1/3 partial cut at SAFE and 75% residual material at EMEND) and 20%–39% residual material (*i.e.*, 20% residual material at EMEND and 2/3 partial cut at SAFE). The rationale is that the 10% and 50% residual material treatments at EMEND were not directly comparable with any treatments at SAFE.

We used nonmetric multidimensional scaling to assess composition differences by region and by treatment type (*i.e.*, harvesting intensity), using the software program PC-Ord (McCune and Mefford 1999). Nonmetric multidimensional scaling is an iterative ordination technique that produces reduced dimensional depictions of species composition from an original, multidimensional dissimilarity matrix. The fit between the collapsed, final solution and its starting matrix is evaluated as stress. As a rule of thumb, stress values as close as possible to 10 yield accurate representations of the species composition in the original matrix (Clarke 1993; McCune and Grace 2002), although patterns resulting from ordinations can still be effectively interpreted with marginally greater stress values. Ordinations were computed using compartment-level data (12 sample units for SAFE, 25 sample units for EMEND) and standardized catch rates for all species across both experiments. These were interpreted in relation to region (EMEND *vs.* SAFE) and harvesting intensity (six harvesting treatments for EMEND and four harvesting treatments for SAFE). We then restricted the data to species common to both experiments and repeated these comparisons. We also completed a trap-level ordination analysis to fully explore sources of variation in the assemblages. This permits an assessment of the extent to which clearcuts may homogenize spider fauna. (Note that "homogenize" is relatively new in the ecologists' lexicon. Here we do not imply permanent loss or extirpation. Rather, we use the term to describe a tight grouping of points in snapshot ordination space, which serves as a warning beacon to assist conservation efforts.) For this, we restricted data to treatments that were directly comparable across experiments (*i.e.*, control, clearcut, 67%–75% residual material, and 20%–39% residual material). Finally, we compared effects of experiment type and harvesting intensity on spider guilds. For all ordinations, a six-dimensional

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solution was first computed to evaluate the optimum number of axes, and then ordinations were recomputed using the appropriate number of axes. A solution from a detrended correspondence analysis was used at the starting point of the ordinations to avoid local minima. Monte-Carlo tests were done on the final solution to test whether our solution could have occurred by chance. *P* values are reported only if less than 0.05.

Species-specific responses by treatment and by region were analyzed using indicator-species analysis (Dufrêne and Legendre 1997). This allowed us to test whether certain species had strong affinities to Quebec or Alberta or to particular levels of harvesting intensity. Resulting indicator values were tested for statistical significance using a Monte-Carlo procedure (1000 permutations) using PC-Ord (McCune and Mefford 1999).

Results

Regional comparisons

Overall, 6107 individual spiders representing 98 species (EMEND) and 3414 individuals representing 86 species (SAFE) were collected. Of these, 44 species were common to the two regions, and the total species count for the two experiments was 139 (full species lists are available from the authors upon request). At EMEND (n = 25) and SAFE (n = 12), 244.3 ± 21.4 (mean ± SE) and 284.5 ± 59.9 spiders were collected per compartment, respectively.

Because the rarefaction curves of the total species collected reach asymptotes prior to the maximum subsample size, our sampling effort adequately captured the majority of the species present in each study area (Fig. 1, inset graph), and the accumulations of species were virtually identical across regions. The lycosid *Pardosa moesta* Banks was the most frequently collected spider in both experiments (Fig. 1). It dominated EMEND (16.4% of the total catch), and was the second most commonly collected species at SAFE (25.4% of the total catch). The lycosid *Pirata montanus* Emerton was the most frequently collected spider at SAFE (Fig. 1). Indicator-species analysis showed that 55 species (of 139) were significant indicators of region at $P < 0.05$. Twenty-nine species were indicators for EMEND and 26 species were indicators for SAFE; this included 17 of the 20 most commonly collected species across both experiments (Fig. 1).

Ordination analyses indicated a clear regional separation of the fauna (Figs. 2*a,* 2*b*); the first axis in both ordinations explained most of the variation in the species-by-sample matrix, and this regional separation was still apparent when data were restricted to species common to both data sets (44 species; Fig. 2*b*). This means that the structure of these common species (*i.e.*, species abundance distributions) varied by geographic location, perhaps because species differing by region played an important role in the relative abundance of species common to each region. The trap-level ordination (Fig. 3) also supported a strong regional effect on the spider fauna from each experiment.

Effects of partial cutting on spider assemblages

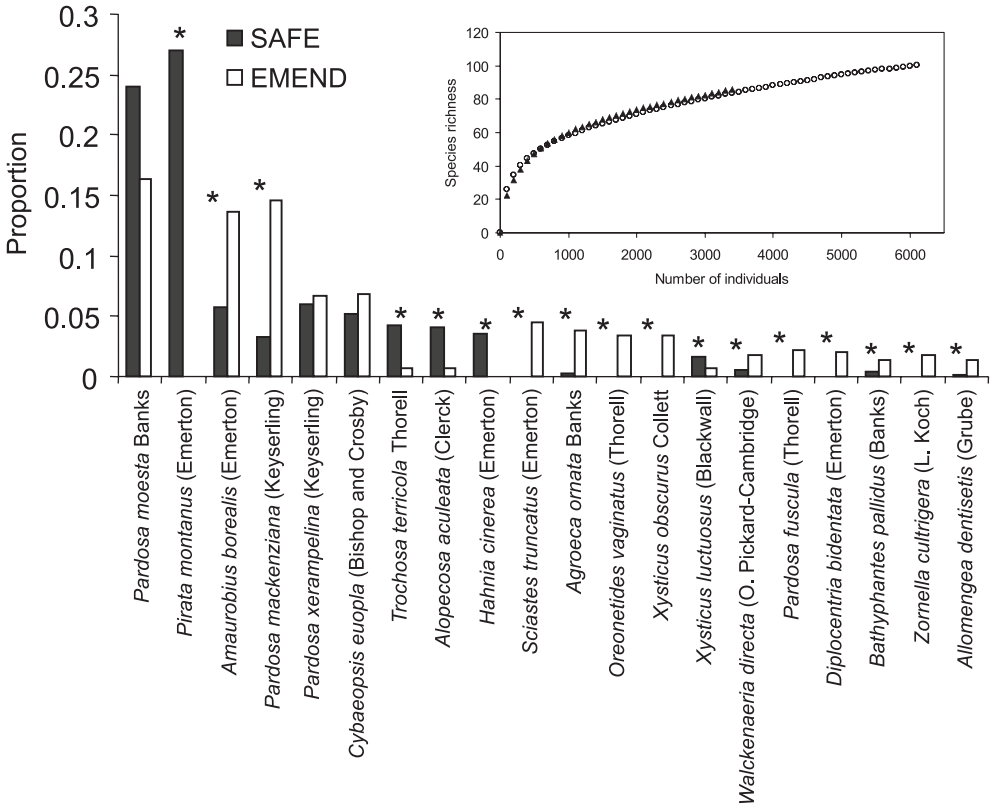
The effect of partial cutting on spider assemblages was assessed first by comparing spider catch rates separately for each experiment using a one-factor ANOVA. There was a significant effect of treatment on catch rates for EMEND spiders ($F_{5,24}$ = 4.05, P = 0.011). Tukey's post-hoc tests (with α = 0.05) revealed that catches of spiders were significantly reduced in control compartments compared with compartments with 50% residual material; all other means were not significantly different from each other. No significant differences in catch rates were revealed for comparisons by treatment at SAFE ($F_{3,11}$ = 1.60, P = 0.264). To assess differences in diversity, rarefied estimates of species richness were compared by treatment types that were most directly comparable across experiments (*i.e.*, control, 67%–75% residual material, 20%–39% residual material, and clearcut). There was much overlap of the 95% confidence intervals when species richness was compared at a standardized level of sampling effort (data not shown). Partial cutting therefore has few discernible effects on spider catch rates and diversity.

Compartment-level ordinations, however, depict a direct effect of partial-harvesting treatments on the composition of spiders for both experiments. Although regional differences represent the first major split along the first axis of the ordinations (*i.e.*, Figs. 2*a*, 2*b*), the second ordination axes separate the fauna by harvesting intensity for all species (Fig. 2*c*) and for the data set restricted to species common to both experiments (Fig. 2*d*). Overall, the control compartments (top of ordinations, highest values along the second axes) harbour a spider fauna

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Fig. 1. Rank-abundance plots of the 20 most commonly collected spiders (representing 86% of the total number of individuals collected) from the SAFE experiment (Quebec) and the EMEND experiment (Alberta); species are ranked according to their catch rates for the two studies combined. An asterisk indicates significant indicator values in either experiment ($P < 0.05$, 1000 permutations). The inset graph shows rarefaction estimates of species richness by sampling effort (number of individuals) for all species collected at SAFE (▲) and EMEND (○); for clarity, standard deviations are omitted.



that is most distinct from the clearcut compartments (lowest values along the second axes), and removal of almost any volume of standing trees causes the composition of the spider fauna to become more similar in ordination space to that in clearcut compartments. Harvesting effects appear more pronounced for the fauna of SAFE than for that of EMEND.

The trap-level ordination, which is constrained to compare only four treatments, also shows a similar pattern, but now the variation explained by the axes is similar for both the first axis and the second axis, and there remains a clear separation of the fauna by region (Fig. 3). Within the regions, however, the composition of the spider fauna from clearcuts is distinct from that of the fauna from control compartments, and there is a clear gradient of effects as partial cutting moves from leaving 67%–75% residual material to leaving 20%–39% residual material (Fig. 3). In general, the fauna from clearcut compartments shows less trap-to-trap variation than the fauna from control compartments, suggesting that 100% removal of standing trees homogenized the fauna, and that this effect is conserved across regions.

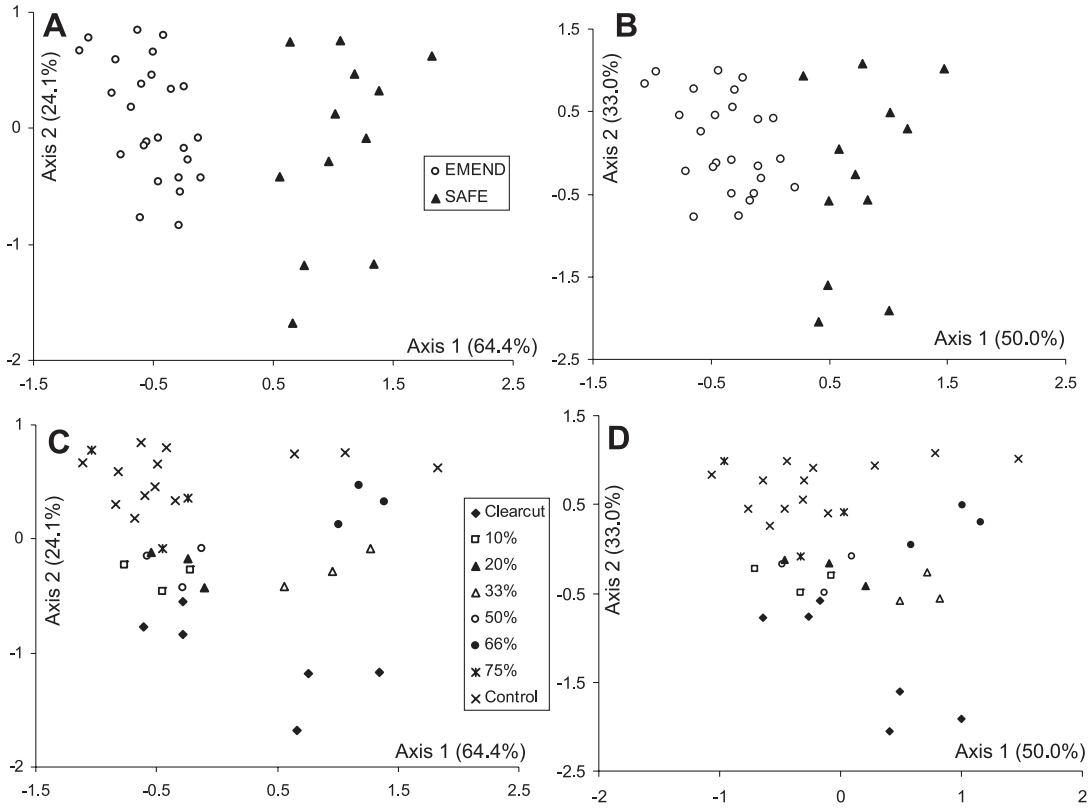
Effects of partial cutting on guilds and species

The ground-running guild (which includes Lycosidae) was numerically dominant in the collections, representing over 50% of the individuals collected (Table 1). However, this guild represents fewer than 20% of the species collected. The second most commonly collected guild was the sheet-web builders (Table 1), which includes such species as the amaurobiids *Amaurobius borealis* Emerton and *Cybaeopsis euopla* (Bishop and Crosby) (Fig. 1). The next most commonly collected guild was the wandering

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Fig. 2. Nonmetric multidimensional scaling ordinations for spider species collected at SAFE and EMEND; each symbol represents a compartment (EMEND, n = 25; SAFE, n = 12). Data were standardized and ordinations either included all species (A, C) or were restricted to the 44 species common to both experiments (B, D). Percent variation explained by each axis is given adjacent to the axis; 50 runs with real data were done for both ordinations. Final stress for ordinations A and C was 11.7, with 73 iterations; final stress for ordinations B and D was 14.0, with 87 iterations. Ordinations were significantly different from random (Monte-Carlo test, $P < 0.05$).



sheet/tangle weavers; this guild represented almost 50% of the total species count. The elevated species richness in the latter guild is expected because it includes Linyphiidae, noted for its remarkable diversity in northern latitudes (Marusik and Koponen 2002; Buddle and Draney 2004)

Ordination analysis of the guild-level data depicts an effect of partial cutting on spider guilds, and most of the variation with this ordination is along the first axis (Fig. 4). Moving from right to left along this axis shows a shift in guild composition from control compartments to compartments that were clearcut, and the various partial-cutting treatments generally occupy the ordination space midway between these two extremes (Fig. 4). Unlike the trap-level ordination, however, the clearcut compartments tend to support more diverse composition, and it is the control compartments that tend to exhibit more homogeneous guild composition (Fig. 4).

We completed a one-factor ANOVA on catch rates for the ground-running and wandering sheet/tangle weavers by treatment type for each experiment separately. At EMEND, there was a significant effect for both ground runners ($F_{5,24}$ = 12.6, $P < 0.01$) and wandering sheet/tangle weavers ($F_{5,24}$ = 5.75, P = 0.02). The ground runners were collected most commonly when over 50% of the standing trees were removed (Fig. 5*a*). The wandering sheet/tangle weavers showed the opposite pattern, as significantly fewer members of this guild were collected in clearcut than in control compartments and 75% and 50% residual material treatments (Fig. 5*c*). ANOVAs of these guilds at SAFE were all nonsignificant ($F_{3,11}$ = 3.21, P = 0.08 for ground runners and $F_{3,11}$ = 0.21, P = 0.88 for wandering sheet/tangle

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Fig. 3. Nonmetric multidimensional scaling ordinations for spider species collected at SAFE and EMEND; each symbol represents a single pitfall trap placed in compartments that differed in harvesting intensity. The dotted line represents the distinction between EMEND and SAFE pitfall traps. Data were standardized and included all species collected. Percent variation explained by each axis is given adjacent to the axis; 50 runs were done with real data; final stress was 16.7, with 58 iterations. Ordination was significantly different from random (Monte-Carlo test, $P < 0.05$).

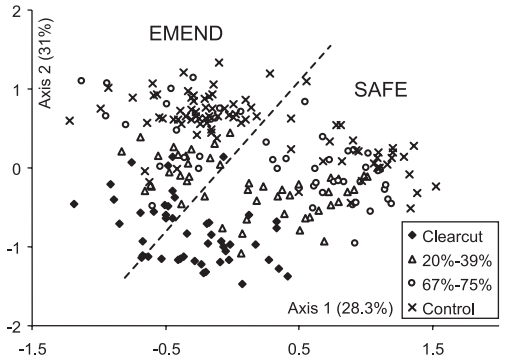
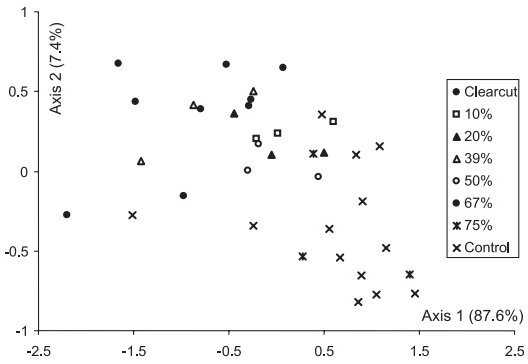


Fig. 4. Nonmetric multidimensional scaling ordinations for spider guilds collected at SAFE and EMEND; each symbol represents a compartment that differed in harvesting intensity. Percent variation explained by each axis is given adjacent to the axis; 50 runs were done with real data; final stress was 7.4, with 89 iterations. Ordination was significantly different from random (Monte-Carlo test, $P < 0.05$).



weavers) (Figs. 5*b*, 5*d*), although catch rates for ground runners were greatest in clearcut compartments at SAFE (Fig. 5*b*).

Indicator-species analysis was done using treatments that were most closely comparable across experiments (*i.e.*, control, clearcut, 67%–75% residual material, and 20%–39% residual material), using data from the two experiments combined. No species were found to indicate control compartments or 20%–39% residual material compartments. Four species were good indicators for treatments with 67%–75% residual material, and 10 species were significant indicators of clearcut compartments. The latter group included the ubiquitous *P. moesta* and *Pardosa xerampelina* (Keyserling) (Fig. 6). We also plotted the catch rates for four additional species to illustrate the broad range of effects (for both region and treatment) (Fig. 6). For example, some species, such as *A. borealis*, were common to both experiments, and showed a decrease in catch rates as harvesting intensity increased. The wandering sheet/tangle weaver *Sciastes truncatus* (Emerton) was infrequently collected in SAFE, but was strongly associated with control compartments at EMEND. In contrast, the sheet-web builder *Hahnia cinerea* Emerton was seldom collected at EMEND, but was most commonly associated with control compartments at SAFE, and its catch rates decreased in comparison with those in all other treatment types (Fig. 6).

Discussion

Our results represent the first broad description of the effects of alternative silvicultural strategies on spider assemblages in deciduous stands in North American boreal forests. These results are valuable because they illustrate how cooperation between stewards of geographically separated large-scale forestry experiments can lead to the formulation of general principles. We have documented a strong regional influence on the local spider fauna in each ecoregion and have shown that partial cutting disrupts the spider fauna in a predictable manner in both regions. We have evidence that clear-cutting homogenizes the fauna, and that clearcuts tend to promote the establishment of generalist hunting spiders; across the country, the same species tend to associate with open habitats created by clear-cutting. Spider guild diversity is also affected by partial cutting, and we have documented species-specific effects that highlight the importance of maintaining closed-canopy stands on the land base.

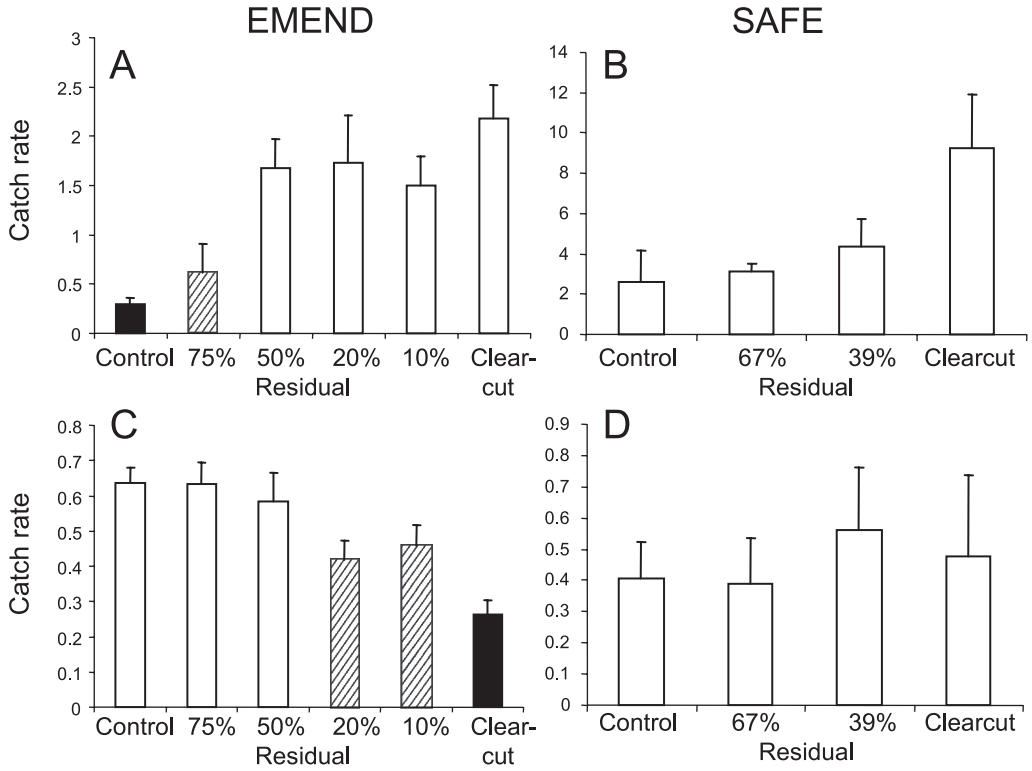
Faunal comparisons by region

Our first objective was to investigate the regional differences between the spider faunas in the boreal plains of Alberta and the boreal shield of Quebec. Only 44 of the 139 species

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Fig. 5. Standardized catch rates (individuals/trap-day; mean + SE) for two guilds: ground-running spiders (A, B) and wandering sheet/tangle weavers (C, D) collected at EMEND and SAFE in compartments differing in harvesting intensity. Significant differences in catch rates are depicted for EMEND collections for both guilds; solid bars *versus* open bars represent significantly different means (Tukey's post-hoc test, $\alpha = 0.05$).



(32%) collected occur in both regions, and the community composition as depicted using ordination analyses and indicator-species analysis separated the boreal-shield fauna from that in the boreal plains (Figs. 1, 2*a*, 2*b*, 3). Regional effects remained distinct even when analyses were constrained to species occurring in both regions. This suggests the existence of significant and important region-specific assemblage structure and composition.

There are, however, two important similarities between the spider faunas of Alberta and Quebec. First, the species-accumulation curves (Fig. 1, inset graph) were virtually identical. This suggests that the ground-dwelling spider fauna may be remarkably similar in overall richness across much of the boreal mixedwood region of Canada. Second, we documented several commonly collected species that show no regional specificity, including *P. xerampelina*, *P. moesta*, and *C. euopla*. The latter two species have also been documented as being among the most commonly collected species in clearcuts and aspen forests, respectively, in central Canada (northwestern Ontario) (Pearce *et al.* 2004). *Pardosa xerampelina* and *P. moesta* have also been shown to be abundant in clear-cut and disturbed sites in boreal forests of eastern Quebec (Larrivée *et al.* 2005).

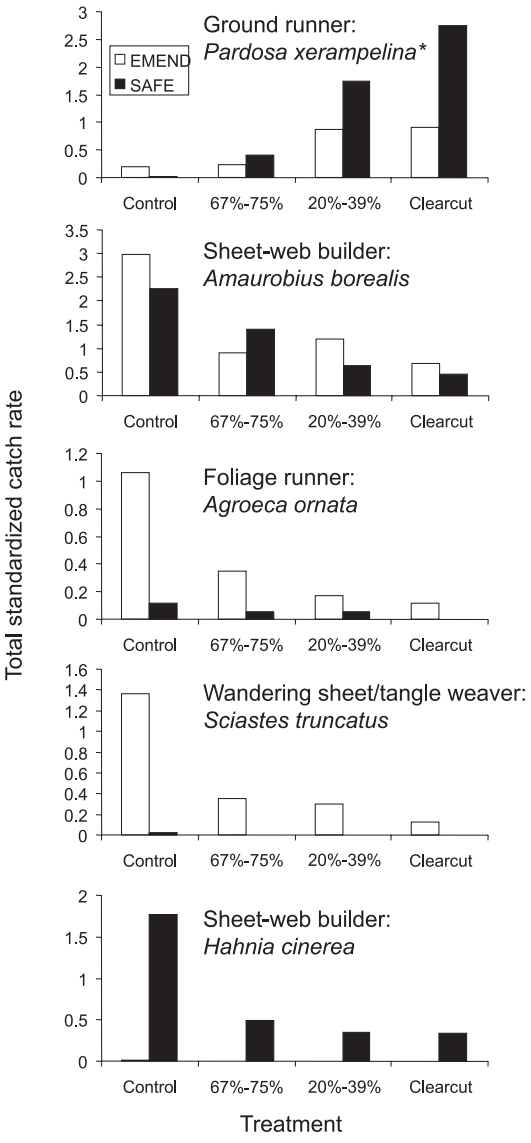
Effects of partial cutting

Our second and third objectives were to investigate differences between the spider faunas of EMEND and SAFE with respect to partial cutting. Overall effects on diversity and catch rates (*e.g.*, ANOVA on abundance and species richness, and rarefied species richness estimates) were relatively trivial and uninformative, which was not unexpected given the lack of information contained in such metrics (Simberloff 1999). In contrast, compositional differences, in which species identity is important, provided important insights. We offer several lines of evidence that removal of 25%–33% of standing stems has distinct and predictable effects on the composition of the spider fauna in deciduous boreal forests of Canada. The second ordination axis resulting from the compartment-level ordinations for all species

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Fig. 6. Standardized mean catch rates (individuals/trap-day) for two representative species from five guilds from control, 67%–75% residual material, 20%–39% residual material, and clearcut compartments at EMEND and SAFE. The asterisk indicates that *Pardosa xerampelina* is a species with a significant indicator value, *i.e.*, this species is a significant indicator of clearcut stands ($P = 0.02$).



(Fig. 2*c*) depicted a shift in spider assemblages as soon as trees are removed. Both experiments showed a gradient from closed-canopy control compartments (top of graphs) to the exposed clearcut compartments (bottom of graphs). The same effect was observed when the data were constrained to species common to both experiments (Fig. 2*d*). This leads to an important generality about the effects of partial harvesting. Certain species whose subpopulations may be over 3000 km apart have similar associations with deciduous cover classes in the boreal mixedwood forest, and have identical responses to partial and complete forest removal.

There were some differences in the amplitude of the effects at SAFE and at EMEND. In particular, compartment-level and trap-level ordinations showed greater variation in relation to treatment types at SAFE than at EMEND (Figs. 2*c*, 2*d*, 3), and catch rates for spiders at EMEND were significantly affected by treatment type. We believe that these differences may be accounted for by the difference in post-harvest collection times. Spiders at SAFE were collected 6 years after harvesting, whereas EMEND spiders were collected 2 years after treatments were established. Short-term effects of forest cutting on catch rates for spiders at EMEND may still be apparent 2 years after harvest, especially since some of the common species in this system take 2 years to complete development (Buddle 2000). Compositional differences in relation to harvesting, however, may take longer to fully establish, and are likely to persist for many years (Buddle *et al.* 2000, 2006). Thus, we might predict that faunal differences at EMEND will increase over time, and may align closely with results from SAFE once additional post-harvest collections are analyzed.

Our results on the effects of partial cutting fit well with the known effects of removing forest canopy on spider assemblages (McIver *et al.* 1992; Pajunen *et al.* 1995; Buddle *et al.* 2000; Pearce *et al.* 2004). There tends to be a distinct fauna associated with closed-canopy forests, and this fauna often comprises web-building species (*e.g.*, in families Amaurobiidae, Hahniidae, and Linyphiidae). As soon as the canopy is opened, diurnal hunters are prominent. Interestingly, in partially harvested compartments, open- and closed-canopy faunas blend quickly and persistently. Any removal of trees shifts the fauna from that found in closed-canopy forests, and this effect remains apparent 2 years (EMEND) and 6 years (SAFE) post harvest. We expect that differences will remain until the secondary forest matures (*i.e.*, >30 years post harvest) (Buddle *et al.* 2000), and (or) saplings establishing in the partial-cut

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corridors are able to reduce exposure and fully close the canopy.

Our second line of evidence rests on the trap-level ordinations (Fig. 3). We still observe important regional effects, but we also document that trap-to-trap variation is less in clearcuts than in other treatment types; this is similar to findings by Larrivée *et al.* (2005), who collected in black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) forests of Quebec. In contrast, Buddle *et al.* (2006) documented a more variable assemblage in clearcuts than in closed-canopy forests. This discrepancy may be explained by spatial scale. Larrivée et al. (2005) collected spiders at a small spatial scale (<600 km^2), whereas Buddle *et al.* (2006) collected spiders across a region of Alberta encompassing over 10 000 km^2. Nevertheless, within the SAFE and EMEND experiments, it appears that clear-cutting acts to homogenize the ground-dwelling spider fauna. Pitfall traps placed in control compartments exhibit the greatest variation along both ordination axes, and this suggests that there are important microhabitat differences that are not present after forest harvesting. It is known that spiders are strongly associated with habitat characteristics of older forests, including coarse woody debris (Buddle 2001; Varady-Szabo and Buddle 2006), and that the volume of dead wood is negatively affected by forestry practices (Duvall and Grigal 1999; Siitonen *et al.* 2000). Additionally, the older forests at EMEND and SAFE originated from wildfire rather than clear-cutting, and wildfire may have lasting effects on the spider fauna, perhaps over the course of decades (Buddle *et al.* 2006). This is supported by the location (*i.e.*, in ordination space) of some pitfall traps that were placed in some partial cuts: many of these traps harbour a fauna that is almost indistinguishable in ordination space from that in traps placed in clearcut or control compartments (Fig. 3). At the trap level, there is a noticeable blending of species compositions between treatment types that is not obvious when data are ordinated at the compartment level.

Effects on guilds and species

We investigated the effects of partial cutting on spider guilds, and we document some species-specific patterns. Spider guilds were affected by experimental forest harvesting, as the ordination analysis depicts a shift in guild composition as cutting intensity increases (Fig. 4), but this shift is somewhat more diffuse than that uncovered with species-level data. The second ordination axis explains little of the variation, but the first axis illustrates a gradient from closed-canopy forest (right-hand side) to clear-cut forest (left-hand side), with partial-cutting treatments falling between the two extremes (Fig. 4). In contrast to what was observed with species-level data, clear-cutting does not appear to homogenize spider guilds; here, spider guilds are more diverse in clearcut compartments than in control compartments.

Many of the patterns are explained by what is happening with the ground-running guild (which includes the numerically dominant Lycosidae) and the wandering sheet/tangle weavers (largely spiders within Linyphiidae) (Table 1). Ground runners were infrequently collected in control compartments but dominated the fauna in clearcuts (Figs. 5*a*, 5*b*) for both experiments. In contrast, the wandering sheet/tangle weavers were significantly less commonly collected in clearcuts at EMEND than in control and 75% and 50% residual material compartments. Results from SAFE were nonsignificant, but we attribute this to the shorter sampling window and smaller sample size for SAFE than for EMEND. Patterns at the guild level were expected, based on past findings in North America and Fennoscandia; diurnal hunters, including our ground-running guild, exploit open habitats, whereas web-builders, which often require complex microhabitats in the leaf litter for web placement (Huhta 1971), are indicative of closed-canopy forests (Koponen 1995; Pajunen *et al.* 1995).

Species-specific patterns further support the guild-level analyses, as clearcuts contained 10 species with significant indicator values; this includes the wolf spiders *P. xerampelina* and *P. moesta*, species both previously known to be associated with clearcuts (Buddle *et al.* 2000; Pearce *et al.* 2004; Larrivée *et al.* 2005). These open-habitat generalists respond the same way across the boreal forests of Canada—they are widespread in their distribution and in their general habitat affinities. Species such as *P. xerampelina* occur in closed-canopy forests but remain relatively uncommon until after the forest canopy opens (*e.g.*, Fig. 6, top), a pattern supported by other research (Buddle *et al.* 2000). Interestingly, no species were found that indicated our control compartments; this suggests that region may be having a larger effect

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on the fauna of older forests, and thus the fauna of older forests may be more restricted in their distribution and more specific in their habitat requirements. This is supported by graphically comparing a set of species that exhibit decreased catch rates as harvesting intensity increases (Fig. 6). Web-builders such as *A. borealis* are common to both regions, and show a decline in catch rates as forests are harvested. *Sciastes truncatus* was rarely collected at SAFE, and shows a clear preference for closed-canopy forest at EMEND. Similarly, *H. cinerea* is infrequently collected in Alberta, and shows an affinity to control compartments at SAFE. We hypothesize, therefore, that increased exposure, brought about by both partial cutting and clear-cutting, may permanently shift the dominance structure from habitat specialists to habitat generalists. Future work will have to bring focus to this prediction by uncoupling canopy closure from stand age. However, if the hypothesis is correct, the maintenance of older stand age classes remains critical to conserving the suite of web-building species that may exhibit an affinity to the diverse microhabitats associated with closed-canopy forests in the boreal mixedwood forest.

Conclusions and future directions

We documented a consistent pattern when comparing the effects of forestry experiments on ground-dwelling spiders occurring in two regions of Canada's boreal mixedwood forest. The retention of green trees, through the use of partial cutting, does act to buffer effects on spider biodiversity compared with traditional clear-cutting, but even with relatively modest partial cutting, we found an immediate shift in the spider fauna from one that is typical of old-growth forest to one with species common to clearcuts. The latter species are true generalists, and show the same patterns in both experiments. It is apparent that to best maintain a spider fauna indicative of older *Populus* spp. stands in Quebec and Alberta, leaving more than 75% of standing trees will be required. If we are truly concerned about maintaining biodiversity in Canada's boreal forest, attention must focus on retaining these upper rotation-aged mixedwood stands, as such forests host spider species, assemblages, and guilds that may be threatened by an increase in openings in the forests created by forestry and by edge effects.

There are several key areas that require future research. At present we have little information on the role of spatial scale and variation in microhabitats on the maintenance of spider assemblages in Canadian boreal systems. We can turn to research in Fennoscandia for guidance (*e.g.*, see Niemelä *et al.* 1996), but since our species complement is at most 30% similar to that of northern Europe (Marusik and Koponen 2002), it is time that we link patterns observed at the stand level to processes occurring within stands. However, this is going to require much more information on the natural history of species occurring in boreal zones. The situation is improving, thanks to the continuing publication of life-history information (*e.g.*, Buddle 2000; Pickavance 2001; Buddle and Draney 2004). Of particular importance is further study of the influence of spider dispersal and colonization in determining the local spider fauna occurring within boreal regions. Such insights will provide vital clues to the reasons why certain species appear stenotopic and geographically restricted, whereas open-habitat generalists appear eurytopic and widespread. We can again turn to the European literature for insights, as important techniques have been developed to assess the importance of dispersal in relation to habitat affinities (Bonte *et al.* 2003).

Finally, we must also strive to garner support for the unification of spider data sets from across the boreal forest. Much has been published on spiders occurring in boreal regions, but to begin addressing further questions arising from regional comparisons of the fauna, and the effects of harvesting on spider assemblages, it is important that data be centralized and openly accessible. The Nearctic Spider Database (Shorthouse 2007) may provide a model for this. We hope that some of the generalizations we have discussed can be tested further as databasing evolves.

Acknowledgements

We thank the following companies, funding agencies, individuals, and institutions. For the EMEND work: Daishowa–Marubeni International Ltd., Canadian Forest Products, the Sustainable Forest Management Network of the Networks of Centres of Excellence, Manning Diversified Forest Products, Université Laval, University of Alberta, University of British Columbia, University of Calgary, University of Lethbridge, University of Minnesota, Alberta Sustainable Resource Development, Alberta Research Council, Canadian Forest Service, and

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Canadian Wildlife Service; the following people played key roles in the EMEND experiment: J. Spence, D. Langor, J. Volney, and more than 15 field assistants and over 10 laboratory assistants. For the SAFE work: Les Fonds québécois de la recherche sur la nature et les technologie, Natural Sciences and Engineering Research Council of Canada, Chaire industrielle CRSNG-UQAT-UQAM en aménagement forestier durable, Forêt d'enseignement et de recherche du lac Duparquet, Groupe de recherche en écologie forestière interuniversitaire, Norbord Inc., and Tembec Inc., Ministère des ressources naturelles du Québec, Société de protection des forêts contre le feu, Canadian Forest Service, McGill University, Université du Québec à Montréal, Université du Québec en Abitibi– Témiscamingue. N. Dupérré and E. Bolduc are thanked immensely for their work on spider identifications, and the following people were vital to the success of the SAFE experiment: S. Brais, B. Harvey, Y. Bergeron, P. Drapeau, T. Work, and many other laboratory and field assistants. We also thank P. Paquin, M. Larrivée, J. Pearce, and K. Aikens for their input and D. Langor for his invitation to participate in this symposium, and two anonymous reviewers for helpful comments on the manuscript.

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https://doi.org/10.4039/n07-LS01 Published online by Cambridge University Press