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**THE SUCCESSION OF LITTER-DWELLING ARTHROPOD COMMUNITIES
FOLLOWING DISTURBANCE BY HARVESTING AND WILDFIRE**

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ABSTRACT

Litter-dwelling beetles (Coleoptera: Carabidae and Staphylinidae) and spiders (Araneae) were sampled in aspen-dominated stands originating from clear-cuts and wildfires. Three age classes of stands were represented: 1-2 years, 14-15 years, and 28-29 years following disturbance. Arthropods were sampled using continuous pitfall trapping throughout the field seasons of 1996 and 1997. Over 21,400 specimens representing 221 species were collected over the two year period. Distinct arthropod communities are associated with recently disturbed wildfire and harvested stands. However, wildfire and harvested stands tend to converge on similar species associations by 28 years following disturbance. In general, the succession of litter-dwelling arthropods following wildfire lags behind the succession following forest harvesting, suggesting the trajectories in re-colonization are dependent on disturbance type.

INTRODUCTION

Invertebrates inhabiting soil, litter, and coarse woody debris are vital elements of forest ecosystems. They play crucial and well-documented roles in decomposition of coarse and fine organic matter, nutrient cycling, maintenance of soil structure and regulation of potential forest pests (Petersen and Luxton, 1982; Spence, 1985; Stork, 1990), and thus are thought to influence long-term forest productivity and sustainability. Invertebrates are also important as a food resource for highly valued forest vertebrates (summarized by Wilson, 1992). The extent to which forest invertebrate communities are affected by forestry practices has serious ecological implications, and is of concern to forest managers.

Forest disturbances such as harvesting and fire alter various physical, chemical, and biological factors in the litter and soil (Simms, 1976; Kubin and Kemppainen, 1991; Cortina and Vallejo, 1994). These alterations, in turn, modify habitats for the invertebrates living there. This is particularly important in Alberta given the greatly increasing economic development of the forest industry (Peterson and Peterson, 1992; Stelfox, 1995), and in the north, large tracts of virgin forest are now allocated to FMAs and slated for harvest. These developments have generated legitimate concerns about the ecological resilience and sustainability of these forests in the wake of extensive harvesting.

There is currently a widespread movement to embrace a "natural disturbance model" for harvest of forests. Proponents argue that use of harvest regimes resembling the spatial

pattern of disturbances on forested landscapes will ensure conservation of biodiversity while permitting extraction of economically desirable volumes of fiber (Hunter, 1993; Bunnell, 1995). In Alberta, harvesting is to be modeled mainly after wildfire, as this is the most obvious and most easily re-constructed of several possibly important disturbances. Despite the logical appeal of the natural disturbance model, it has not been well tested (Alpert, 1995) and it clearly embodies several oversimplifications (Haila, 1994). Hence, there is a need to determine whether succession from burned and logged sites generates forest structure suitable as habitat for the normal mixedwood biota.

To contribute towards this knowledge base, and to specifically test the natural disturbance model, we have investigated the relative effects of harvesting and fire on beetle (Coleoptera) and spider (Araneae) assemblages associated with soil and litter in aspen-dominated mixedwood forests in north-central Alberta. Beetles and spiders are ideal organisms for understanding the effects of disturbances on forest ecosystems as they are among the most conspicuous and abundant groups of arthropods in forest ecosystems. Beetles and spiders also are highly sensitive to habitat changes (e.g., Niemelä, 1990; Uetz, 1991), especially those resulting from forest cutting (Huhta, 1971; McIver et al., 1992; Niemelä et al., 1993; Spence et al., 1996). Because of their sensitivity to environmental variation, beetles and spiders are potentially good indicator species for assessing the effects of habitat perturbations, and a detailed study of their assemblages may provide an effective model of arthropod response to forestry practices.

The research reported here has been executed in the context of a larger multi-disciplinary, multi-agency project titled "The effect of wildfire and timber harvest residuals on biodiversity, and forest stand/landscape structure in aspen-mixedwood communities in Alberta" commenced in 1995 under the leadership of P. Lee at the Alberta Environmental Centre. The objective of the research reported here is to understand how rove beetle (Staphylinidae), ground beetle (Carabidae), and spider assemblages change over time since disturbance, and identify faunal components that may be particularly sensitive to differences between burning and harvest.

METHODS

A total of 12 stands in the boreal mixedwood region of Alberta were studied. The forests in this region are dominated by trembling aspen (*Populus tremuloides* Michx.). Six of the stands regenerated naturally after wildfire and six regenerated without intensive silvicultural intervention after harvest. Collectively, three age classes were represented, with stand origin in approximately 1995, 1982, and 1968.

Litter and ground-dwelling taxa of the three taxonomic groups were sampled using continuous pitfall trapping in 1996 (year 1) and 1997 (year 2). One trap-line, consisting of six pitfall traps placed 50 m apart, was placed in each stand. Traps were white plastic containers 10 cm in diameter, containing a preservative and protected from rain with an elevated plywood cover (see Spence and Niemelä, 1994 for details).

RESULTS

A rich database resulted from two years of fieldwork. More than 21,400 individual arthropods representing 221 species have been identified. This includes 6,194 ground-beetles representing 38 species, 7,840 rove beetles representing 76 species and 7,387 spiders representing 107 species.

Cluster analysis of the widely-used Bray-Curtis index, based on the relative abundance of species, is used to illustrate the overall pattern of similarity for these invertebrate assemblages with respect to stand age and origin combinations. Overall, the results suggest that pyrogenic and harvested stands tend to converge on similar species associations over time as the highest similarity values generally occur among the older stands (Fig. 1). The two treatments originating in 1995 were the most dissimilar compared to the combined sample from older treatments. This underscores that the litter-dwelling invertebrate fauna is profoundly affected by disturbance and that traditional harvests and wildfire affect the faunal in rather different ways. The highest similarity was between the 1968-Fire and 1982-Harvest samples, suggesting that pyrogenic stands lag behind harvest-origin stands in faunal recovery.

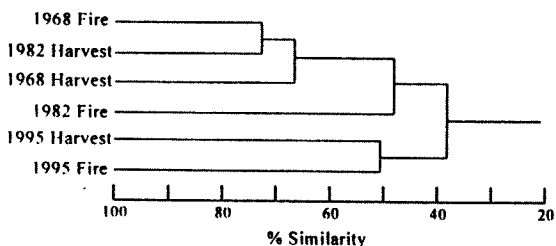


Fig. 1. Cluster analysis of Bray-Curtis measures of percent similarity for beetles and spiders collected by pitfall traps in year 1 and 2

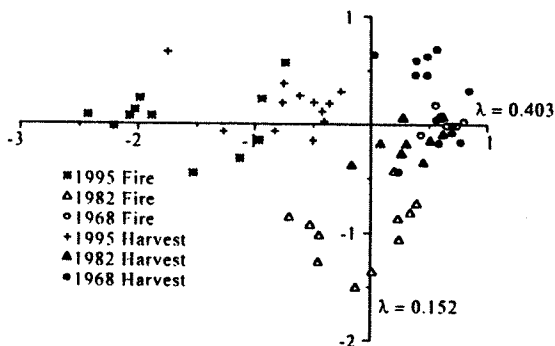


Fig. 2. Sample scores (pitfall traps) from DCA ordination from 218 species of beetles and spiders collected in year 1 and 2

Results from a detrended correspondence analysis (DCA) depicts individual trap data about all three taxa in ordination space defined by the first two DCA axes (Fig. 2). The convergence of faunal assemblages from the 1968-Fire and the two oldest harvest-origin sites is apparent. As would be expected from the results of the cluster analysis, the 1982-Harvest and 1968-Harvest stands are closer together in the ordination than are the comparable fire-origin stands. Fire- and harvest-origin assemblages start off from overlapping points in the ordination-space, and they appear to follow diverging trajectories

before finally converging in the oldest stands. Thus, both cluster analysis and ordination support the claim that litter invertebrates converge with respect to general community structure by 28 years post-disturbance. However, given that the two chronosequences followed quite different trajectories to reach the present positions in ordination space, it is risky to predict that community development will be parallel in fire- and harvest-origin stands in the future.

Some species of each taxon are collected only in stands of one age or origin type. In summary, 87 species were unique to one stand origin type. Overall, 36 species or ca. 41% of the unique species, were found only in fire-origin stands, and 51 species were collected only from harvest origin stands. Most (81) of these are records of 1-5 individuals and must be presently discounted because biological understanding is insufficient to interpret the meaning of their presence. These may be rare species with unique habitat requirements, but alternatively could be stragglers captured at particular sites mainly through chance.

Six relatively common species (5 carabids and 1 spider), however, were more abundant in stands of a single origin type. The carabid, *Nebria gyllenhali*, was found only in 1968-Harvest stands. Four carabids, *Elaphrus lapponicus*, *Harpalus egregius*, *H. laticeps* and *Platynus mannerheimi*, were collected only from fire origin stands. All but *P. mannerheimi* were found in the youngest pyrogenic stands; the two *Harpalus* species were restricted to these but *E. lapponicus* was also taken in the 1982-Fire stands. *P. mannerheimi*, on the other hand, was found only in the oldest fire-origin stands. The spider, *Gnaphosa borea*, was restricted to pyrogenic stands but was found in all three age classes of this stand origin type.

DISCUSSION

Recently burned and recently harvested stands are quite dissimilar to most observers. The question for those interested in managing forests in the context of the new emerging sustainability criteria is whether such differences throw biotic succession onto different courses that might threaten some of the biota. The data presented aim to determine how close succession from burns and harvests might be in the aspen-dominated mixedwood to assess whether harvest was a reasonable substitute for fire with respect to development of the litter-dwelling invertebrate fauna. If so, it is reasoned that fire- and harvest-origin stands may develop increasingly similar faunas as they aged. If the fauna diverged significantly, however, the logic of using harvest as an analogue for fire may be flawed.

Data from this study support the general thesis that epigeaic arthropod assemblages in harvest-origin stands become increasingly similar to those of fire-origin stands with time. Clearly, the abundance and species composition of the epigeaic fauna of aspen-dominated mixedwood stands becomes increasingly similar between harvest- and fire-origin stands over a 30 year period after stand-initiating disturbance. However, conclusions about how closely former harvests have resembled wildfires as stand initiation processes depends on how the results about faunal development are weighed. Furthermore, a convergence in faunal assemblages does not imply a complete overlap of the fauna following the two disturbances. The trajectories in re-colonization differ in young wildfire and harvest stands, and it is premature to state that there is a full recovery after ca. 30 years post disturbance.

Six reasonably common species were identified as strongly associated with either burned or harvested stands and data about them provide the strongest contrasts between harvest and wildfire as stand initiating processes. Furthermore, biological information is

available for some of these species, offering basis for conjecture about the meaning of the data.

Of the six common species unique to one origin type, only a single carabid species, *Nebria gyllenhali*, was abundant and unique to harvest origin stands. All specimens were taken from a single 1968-Harvest stand suggesting possible influence of a local site effect. *N. gyllenhali*, as is the case for many *Nebria* species (Spence, 1979), is usually found in riparian situations. The presence of *N. gyllenhali* in the samples from the 1968-Harvest sites probably reflects the proximity of the traps to wet or riparian areas.

The five remaining species that were both commonly collected and unique to a stand-origin type were found only in fire-origin stands. These include *Harpalus egregius* and *H. laticeps*, characteristic of early successional communities. These species may depend on fire to generate suitable habitats. The other two carabids, *Elaphrus lapponica* and *Platynus mannerheimi*, are both strongly associated to with wetter forest patches although neither is strictly riparian. The spider *Gnaphosa borea* was found only in fire-origin but over the full range of stand ages. Published information about the biology of *G. borea* is limited but it is known mainly from wetter sites in Canada (Platnick and Dondale, 1992). These species might then be excellent indicators of the suite of conditions associated with stand initiation by wildfire. The persistence of such species could be threatened on landscapes dominated by harvesting, especially if fire suppression is effective enough to prevent large, contiguous areas of mixedwood forest from burning over long intervals. Silvicultural practices on harvest-origin stands that kept these species in the system would improve the emulation of natural processes with respect to faunal development.

Harvesting practices in upland areas should be adjusted to ensure that a range of sizes representing wetter microsites are left undisturbed. In a number of northern forest types throughout the world it is being recognized that isolated wet forest patches, often skipped by wildfires, provide important storehouses for biodiversity (Anglestam, 1997). Not only are these centers for species with habitat preferences for wet areas, but these sites may also retain deep-forest specialists in cutovers, facilitating rapid re-colonization with canopy closure. These features characterize part of the epigeic fauna of the boreal mixedwood, and negative faunal effects can be reduced by ensuring that a suitable range of wet patches are left in the wake of logging.

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