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A SHORT-TERM STUDY OF THE FAUNAL ASSOCIATIONS IN OLD WHITE PINE ECOSYSTEMS

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Abstract

This study was conducted to assess the value to wildlife of white pine (Pinus strobus) ecosystems in Ontario as a response to public concerns over the diminished amount of old growth pine in the province. Five taxa were chosen for study: small mammals, carabid beetles, ants, salamanders, and resident birds in winter. Three questions were addressed: 1) does the fauna associated with old-growth white pine differ from the fauna of other old-growth forest types?; 2) does the fauna of old growth white pine differ from that in mature white pine?; and 3) does the fauna in white pine depend on location of the stand within the province? Three study regions were selected in northwestern Ontario, north of Atikokan; northeastern Ontario, north of Espanola; and Algonquin from Dacre to Whitney. There were no suitable old-growth pine sites in the Algonquin region, but all three treatments were present in the northeast and northwest: old-growth pine, mature pine, and old-growth 'other' forests. Winter-resident birds were only measured in the northeast, and data for the other four taxa were collected from the each region. Data from all test organisms indicated that location in the province affected faunal community composition. In particular, there were large differences between the northwest, and the other two study regions. We found no species that only occurred in white pine in any region, but communities of ants and salamanders in some regions were different between white pine and 'other' forests. Similarly, although there were no dramatic and universal differences between old-growth pine faunas and those in mature pine, ant and salamander community structures differed somewhat between these two age classes of pine. There was no evidence that forest type affected the species composition of winter-resident birds, but an exceptionally mild winter and late start of field work may have influenced the results. Different forest types supported somewhat different animal communities, but there was no strong evidence to support maintaining old-growth pine specifically for its associated animal fauna. However, managers should retain white pine ecosystems everywhere that they occur to protect the biodiversity of Ontario.

Introduction

Problem definition

Forests dominated by red pine (*Pinus resinosa*) and white pine (*Pinus strobus*) were the dominant coniferous forest type throughout the Great Lakes-St. Lawrence forest at the time of colonization of Canada by Europeans. Logging of pines created a major industry in Ontario (and in other provinces) from the early-1800s until the mid-1900s, and most of the mature pine is now gone (Aird 1985). Our study was initiated as part of the response by the Ontario Ministry of Natural Resources and the Canadian Forest Service to public concerns over the loss of ecosystems dominated by red pine and white pine, particularly in the old age classes. Concern for the loss of 'old-growth' forests is universal in North America (eg., Maser 1990, Ont. Old Growth Policy Advisory Comm. 1993, Noss and Cooperrider 1994).

Welsh et al. (1992) prepared a background paper for this research. Their study was based on a questionnaire to forest-wildlife experts that asked questions about which species could be most affected by the loss of old pine forests. They further emphasized the mission-oriented nature of this study with respect to the pertinent management perspectives. As forests age, their characteristics change. Many old-growth forests, with their gap dynamics and accumulations of woody debris, have different animal species diversities and communities than those in younger forests, even when compared with the mature stage (Ruggiero et al. 1991). Our research program was conducted to assess the importance of old white pine forests to wildlife species.

The following null hypotheses formed the basis for our study:

1) forests dominated by white pine contain faunal diversity similar to other forest types once the mature stage has been attained;

2) once pine forests have matured, no changes in faunal diversity can be expected as the forests become old-growth.

Stand conditions may be affected by location of the stand in Ontario, by various stand attributes (e.g., species composition, site factors, topography, stand size, debris, canopy), and by landscape variables (e.g., proportion of pine in the landscape, distance among stands, stand size). Aside from questions relating to stand age, we were also interested in the question of animal species composition with respect to stand location in the province: if managers are to maintain old forest, does location within the province affect animal community structure (ie., in terms of fully functioning ecosystems)? Therefore the final null hypothesis tested was:

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3) the diversity of species and animal community structure in white pine systems are similar along gradients from north to south and from west to east, in Ontario.

Based on the report by Welsh et al. (1992) and discussions among various wildlife experts, the animal communities chosen for the study included: carabid beetles, ants, small mammals, and winter-resident birds. We collected data incidentally for salamanders (from pitfall trapping). In 1993, a cross-Ontario survey of remaining pine forests was conducted to choose suitable study sites (Jung and Thompson 1993). From sites found during that survey, and based on locations previously used for vegetation work (Carleton and Arnup 1993), and for songbird studies (D.A. Welsh, Canadian Wildlife Service, unpublished data), pine stands were chosen for our faunal study. This interim report includes an analysis of data collected during one field season, and has provided the basis for a more intensive study at one location (Rushbrook Lake), during the next 2 to 3 years. The study taxa are discussed individually and the results are drawn together in a final general conclusions section.

Study taxa

Small mammals select habitat based on various stand qualities and structures (Dueser and Shugart 1979, Adler 1987, Andren 1994). Small mammal community structure may be affected by habitat structure (Miller and Getz 1977, Dueser and Shugart 1979), food availability (Sullivan and Krebs 1981), and competition (Hoyle and Boonstra 1986, Hallett 1991), and some or all of these factors may be altered by forest harvesting (Martell 1983, Monthey and Soutiere 1985). Although several of the species common in forests of Ontario appear to be somewhat generalized in their habitat selection (Martell 1983), differences in habitat structure among forest types and between pine stand ages may be sufficient to affect small mammal community structure. The communities are relatively simple to sample, and species biology is somewhat understood for several of the species.

The Carabidae are a group of terrestrial beetles whose populations, distributions, and spatial and temporal dynamics have been widely studied. This is a result of both the relative ease of sampling and available taxonometric monographs (Lindroth 1961, 1963, 1965, 1968, 1969). It is widely accepted that these insects show non-random distributions within and between habitat types (Spence and Niemela 1994). Intensive research in Scandinavia and western Canada (Buse 1988, Niemela et al. 1988, 1993, 1994, Erikstad et al. 1989, Haila et. al. 1994) has indicated that carabid communities are structured within forest types according to patches of microhabitat.

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These attributes make carabid beetles excellent candidates for studies that attempt to relate forest stand structure to habitat selection (Kremmen et. al. 1993). General habitat requirements have been determined for many Canadian species of carabids (Lindroth 1961, 1963, 1965, 1968, 1969), although the described associations are too broad (e.g. "forest" or "field" species) to be useful in defining habitat requirements at the levels of stand seral stage or species composition. Few studies have been carried out to determine whether specific forest habitats are inhabited by particular carabid species assemblages in North America (e.g., Niemela et al. 1993), and there are none from the Great Lakes-St. Lawrence forest region.

Ants (Hymnoptera) occupy a wide variety of ecological niches in many habitat types, including forests. Their nesting behaviour restricts individual species to a limited number of habitats (Vepsäläinen and Pisarski 1982). Although most ants in northern latitudes primarily nest in the soil (Savolainen et al. 1989), carpenter ants (*Camponotus* spp.) typically nest in decayed or damaged wood, such as snags and woody debris (Sanders 1964, Sanders and Pang 1972, Sanders 1977). Punttila et. al. (1994) and Sanders (1970) reported that the abundance and diversity of ant communities decreased with an increasing stand age, in northern coniferous forests. Punttila et al. (1994) found that while old-growth coniferous forests did not harbour as rich an ant fauna as did younger forests, some species were old-growth specialists. Ants were a chosen taxa for this study because: some species may be habitat specialists and select certain structural features inherent in old-growth forests, there is no seasonal succession of ant communities in northern forests (Savolainen *et al.* 1989, Punttila *et al.* 1991) thus simplifying data collection, and ants are relatively easy to sample quantitatively.

Species of forest songbirds are well known to differ among forest types based on the structural complexity of the habitat (MacArthur and MacArthur 1961, Erskine 1977). These patterns of species composition and relative abundance by habitat are altered substantially by logging, with effects at the stand level (Franzreb 1975, Titterington et al. 1979), and at the broader landscape level (Angelstam 1992, Andren 1994, Monkkonen and Welsh 1994). Although there have been numerous studies on the use of habitat by neotropical migrants there is little information on resident forest birds. Many resident bird species depend on broad areas of forest, and some require coniferous seeds that may occur irregularly. Monkkonen and Welsh (1994) recently proposed that resident birds may be at substantial risk because of habitat loss and the conversion of broad tracts of mature forest to younger deciduous stands. We studied resident birds because of the potential of structural features and seed production in

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mature conifers to influence the presence and abundance of these species.

Terrestrial woodland salamanders are an important vertebrate component of forest ecosystems. Burton and Likens (1975a) calculated that the salamander biomass of a northern hardwood forest in the Hubbard Brook ecosystem was 2.6 times greater than that of breeding birds and equal to that of small mammals. The role that salamanders play in nutrient cycling and forest food webs is not well recognized by forest managers (Burton and Likens 1975a, b, Pough et. al. 1987, Corn and Bury 1991). Despite the importance (and possible keystone role) of salamanders in forest ecosystems few studies have been published. Welsh (1990) found that Plethodon elongatus and Rhyacotriton olympicus were present in old-growth Douglas-fir (Pseudotsuga menziesii) forests, but absent in early successional and mature forest stages. Scott and Ramotnik (1992) observed that Aneides hardii were more abundant in old-growth mixed-conifer stands than in mature or logged stands. Petranka et. al. (1993) found that the abundance of salamanders in uncut stands was 5 times greater than in adjacent clearcuts.

Our report includes a general narrative of methods, followed by separate results and discussion for each taxon, and a final general discussion section with recommendations for white pine forests in Ontario.

Methods

Study areas

Study sites were chosen in three general regions: in Northwestern Ontario, north of Atikokan near White Otter Lake (northwest); in northeastern Ontario, north of Espanola at Rushbrook Lake (northeast); and in eastern Ontario from the Madawaska highlands to Algonquin Park (collectively referred to as 'Algonquin') (Figure 1). We standardized several variables that might have influenced wildlife species composition by setting the following criteria for stand selection: the minimum stand size was 50 ha, the stand was not entirely isolated from other mature forest, the pine content by stem density was between 40 and 90% and was predominantly white pine, the deciduous component was between 10 and 30%, the site quality was medium to good (i.e., not on shallow or rocky soils), the stand had never been logged, stands were on rolling topography, and the age was >90 years for mature and >120 years for old growth. We also chose control stands to meet similar criteria but the conifer content was comprised of locally-abundant coniferous species other than red pine or white pine.

At White Otter Lake and Rushbrook Lake we were able to locate 5 stands in each of our pine treatments, whereas no old-growth stands met our criteria in the Algonquin area. Because the Algonquin area was located over a radius of 40 km at Dacre, Whitney, and Petawawa, we used 7 mature pine stands (rather than 5) to account for possible regional variability. Sufficient control stands were difficult to locate because of past logging operations. We chose 4 control stands in Algonquin and at Rushbrook Lake, and 5 stands at White Otter Lake. Controls in Algonquin were dominated by eastern hemlock (Tsuga canadensis), with white spruce and black spruce (Picea glauca and P. mariana). At Rushbrook Lake and White Otter Lake, the control stands were dominated by spruces, and to a lesser extent by jack pine (Pinus banksiana), and balsam fir (Abies balsamea). The deciduous component in Algonquin was predominantly tolerant hardwoods; in the northeast (Rushbrook Lake) there was a mixture of tolerant and intolerant hardwoods; and in the northwest (Clearwater-White Otter Lakes) the deciduous trees were mostly intolerant hardwoods.

Sampling animals

Small mammals

We sampled small mammals in the spring (May-June) and fall (October) using snap traps. We sampled 2 trap lines at least 300 m apart, with 25 stations each located 10 m apart, with 2 Victor snap traps baited with peanut butter at each station. Lines were run for 3 days. We froze captured animals and analyzed them later to determine: species, sex, weight, age, and number of placental scars in adult females. We reported captures as the number of animals per 100 trap-nights (TN).

Carabid beetles and ants

We trapped each stand for carabid beetles and ants using 20 pitfall traps, at four randomly chosen sites with 5 traps each. Each group of 5 traps was arranged in a square 10 m on a side, with the fifth trap placed in the centre. Traps were circular, with a 10.2 cm diameter, contained approximately 40 ml of 70% ethylene glycol, and were covered by a board raised 2-3 cm above the trap to reduce dilution by rain and incidental captures of small mammals. We set the traps below the surface of the duff layer and opened them for three 10-day periods from late July through August. The contents of each trap were emptied into a plastic bag that contained alcohol and placed in cold storage for later sorting. In the laboratory each sample was cleaned, rinsed, and sorted for ants, carabid beetles, and salamanders captured incidentally. Carabid beetles were pinned and placed in the University of Guelph collection, and

identifications followed Lindroth (1961, 1963, 1965, 1968, 1969). We sorted ants to species level and identifications followed Wheeler and Wheeler (1963), Creighton (1966), Holldobler and Wilson (1990) and Bolton (1994). We reported captures as number/100 TN. Some traps were destroyed by bears and moose at all locations, and by people at sites in Algonquin Park.

For insects, we also trapped additional southerly sites at Charleston Lake Park (2 stands) and at Murphy's Point Park (2 stands). These stands were too small and isolated to maintain populations of small mammals, salamanders or resident birds distinct from those in the surrounding areas.

Salamanders

Accurate sampling of salamander populations is difficult because terrestrial salamanders are semi-fossorial, and their surface activity is largely nocturnal and is influenced by rainy periods. How to sample salamanders is a controversial issue (see: Scott and Ramotnik 1992, Ash and Bruce 1994, Petranka 1994). The controversy involves biases that do not account for differing surface activity levels of salamander species in relation to the time of day or weather, and inter-observational biases in searching for very small animals that can be found on the surface, in and under logs, in crevices, under rocks, in the duff layer, and 2.5 m above the ground on plants. We elected to use the pitfall trapping method because it is non-biased (Aubrey et al. 1988, Corn and Bury 1991), and because salamander captures would be incidental to the concurrent terrestrial arthropod survey. Salamanders were identified following Cook (1984).

Winter-resident birds

We only sampled birds in winter at the Rushbrook Lake area (northeast) because of time and logistical constraints, and the lack of competent observers. We selected 28 0.5 km^2 plots based on forest resource inventory maps, aerial photographs, and our previous ground work in the area. We chose 5 plots in 'other conifer-dominated forest', and 4 plots each in six treatments: white pine-dominated forests covering 25, 50, and 100% of the plot, in two age classes (mature and old growth). One observer censused a plot along four transects 175 m apart by walking for 30 seconds, stopping for 10 seconds, and recording all birds seen or heard. Numbers of birds in flocks were counted by moving off the transect to count the birds. Plots took approximately 3 hours each to census. We have made no effort, in this preliminary report, to standardize numbers of birds recorded based on the amount of time spent on each plot,

or for the effective radius of detection for individual species (e.g., Nilsson 1974). We tested for differences among the seven treatments by species, communities, and feeding guilds. We also combined various treatments for further testing as follows: by age class of pine, pine vs 'other forest', and 'other forest' plus all 25% pine plots vs a single combined treatment for mature and old-growth pine.

Statistical analyses

We examined all data sets (mammals, carabid beetles, ants, birds, salamanders) in a similar manner. Data were clustered to look for patterns in area, stand age, and pine content using an agglomerative procedure (Ward's method). Clustering was done on actual species counts and on the presence/absence matrices. We tested the three stand types, and three regions in the province as treatments. Multiple ANOVAs were calculated based on following nested model to test for differences within individual species:

$$species = stand\ type + region + type*region.$$

We used LSD (least significant difference) tests to compare among individual treatment classes (Day and Quin 1989). Finally, we tested for differences in community structure using discriminant function analysis with individual species as the variables. Community diversity was calculated using the Brillouin diversity index (BDI) (Pielou 1975) and ANOVA was used to test for differences among the treatments.

Results

Small mammals

We captured nine species of small mammals across the province in pine and other stands. The most abundant species were red-backed voles (Clethrionomys gapperi) and deer mice (Peromyscus maniculatus) in all regions and stand types. Field voles (Microtus pennsylvanicus) were only recorded in the northeast, and yellow-nosed voles (M. chrotorrhinus) and heather voles (Phenacomys intermedius) were primarily caught in the northeast (Table 1). Cluster analysis suggested that there were differences between the small mammal community of northwestern Ontario and that of the northeast, but that Algonquin was similar to both based on the total capture data (Figure 2). Clustering of the presence/absence data showed three distinct clusters corresponding to the three regions. Diversity of small mammals was significantly higher in the northeast compared to the northwest ($P_{spring} < 0.005$, $P_{fall} = 0.05$), but not compared to Algonquin in either season. Only one significant difference was noted

among regions or forest types: in the northwest region, the spring diversity in mature pine was significantly higher than in the other two stand types (P = 0.02) (Table 2, Figure 3).

For the two most abundant species, we recorded differences in productivity and population among the three regions. Spring and fall densities of C. gapperi were significantly greater in the northwest than in the northeast, and greater than those in the northeast or Algonquin in the fall (P_{spring} = 0.04, P_{fall} < 0.001), but there was no difference among forest types (Table 1). For P. maniculatus, we found significantly higher numbers in the northwest compared to the northeast and Algonquin in fall (P = 0.01), but there was no difference among forest types (Table 1). C. gapperi and P. maniculatus had significantly lower productivity (mean scars/adult female) in 'other' forest in Algonquin compared to all other treatments (P < 0.01) (Tables 3 and 4). However, we found no difference in productivity within forest types at either of the other two regions or between small mammals in Algonquin pine compared to pine stands at either northern region. Productivity was higher in C. gapperi (P < 0.001) in the northwest than in either other region (Table 3), and was lower for P. maniculatus in Algonquin compared with the northern regions (P = 0.01) (Table 4). Weights of adult male and adult female C. gapperi were significantly greater in the northwest compared to either the northeast or Algonquin (P < 0.0001, for males or females) but there was no difference among the stand types (Tables 3 and 4).

Among the less common species, we captured 9 of 10 M. chrotorrhinus in pine forest (Table 1). Masked shrews (Sorex cinereus) were more abundant in the northwest than in the northeast in spring (P = 0.03), and more abundant in the northwest and the northeast compared to Algonquin in fall (P < 0.001) (Table 1).

We could not discriminate among forest types based on our spring data. However, using fall data and data from both trapping sessions combined, we found significant discriminant function models (Wilks lambda = 0.48 and 0.64, P = 0.06 and 0.006, for fall and combined seasons, respectively). The discriminant model based on our fall data enabled a correct prediction of forest type for 60, 61, and 54% of the forest stands by type for old-growth pine, mature pine, and other forest, respectively. Significant species in this model were M. chrotorrhinus, and S. cinereus. The model based on captures from both seasons combined showed a higher statistical separation among classes, but had somewhat reduced discriminatory power (55, 67, and 42% respectively, for old-growth pine, mature pine, and other forest). The same two species as in the previous model, and the woodland jumping mouse (Napeozapus insignis), were important predictors in the latter model as well.

Spring and fall data resulted in highly significant discriminant functions with high capability to predict mammal communities among the three study regions (Wilks lambda = 0.35, and = 0.18, P < 0.001, for spring and fall, respectively). The fall data was correctly classified using the model for 90% stands from the northwest, 100% of the northeast stands, and 64% of the Algonquin stands. There was no consistency in placement among the few misclassified stands. Significant species in the model from the fall collections were: C. gapperi, Peromyscus maniculatus, Phenacomys intermedius, S. cinereus, and short-tailed shrew (Blarina brevicauda).

Carabid beetles

Pitfall trapping during the 1994 field season resulted in 15,845 trap-nights. This was lower than the potential 23,400 trap days because of human and wildlife interference to traps. We captured 2,024 carabids (12.77 carabids/100 TN), in 13 genera and 23 species, from the three sample periods (Table 5). All species occurred in the first sample, but we recorded only 19 species from across the province during the second and third sample periods. The six most prevalent species were: Synucus impuntatus, Scaphinotus bilobus, Sphaerodaerus lecontei, Pterosticus coracinus, Calathus advena, and Calathus gregarius. These species accounted for 89% of the catch (Table 5). All common species were found in the three regions, and in most cases in all forest types.

Cluster analysis of the catch data suggested distinct clusters for the beetle communities for the northwest and the northeast, but Algonquin was indistinct from northeast (Figure 4). Clustering the presence/absence data provided the same results. We observed no significant differences between sample periods by regions or stand types for the total number of carabids caught (Table 5). We found that catches of several carabid species were significantly different among regions. Synucus impunctatus, P. coracinus, P. adstrictus and C. gregarius were more abundant in northeast and Algonquin than in the northwest (P = 0.04). Calathus ingratus was significantly more abundant in the northeast than the northwest (P < 0.05), or Algonquin (P = 0.02). Sphaerodaerus lecontei and S. bilobus were more abundant in the northwest than in the northeast (P < 0.0001), or Algonquin (P < 0.05).

In addition to the species reported in Table 5, we recorded several species rarely (< 3 individuals) in our sample. Among these, Blemus discus, was found only in the Algonquin region. Three other rare species: Agonum descentis, Cymindis unicolor, and Calasoma frigidum were found only in the northeast. Pterosticus punctatissimus was absent from the northeast, but was found in the two other regions. Myas

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cyanescens was absent from the northwest, and M. coracinus was found only in that region.

Few differences in the number of carabids captured were related to forest type: P. coracinus and C. ingratus were more abundant in mature pine than in old-growth pine stands in the northeast ($P < 0.002$). Diversity (BDI) was not significantly different between regions or stand types (Table 2, Figure 5).

Discriminant function analysis revealed no significant differences among stand types. However, we found a significant discriminant function among regions (Wilks lambda = 0.392, $P < 0.0001$). This model successfully predicted region for 67, 60, and 89% of Algonquin, northeast, and northwest cases, respectively. The significant species in the model were S. inpunctatus, C. gregarius, S. bilobus, and P. coracinus. A second discriminant analysis, using mature and old pine in the northwest and northeast, also yielded a significant model (Wilks lambda = 0.341, $P < 0.0001$). These data were correctly classified using the model for 92% of northeastern stands, and 89% of northwestern stands, with the following important predictor species: Sphaerodaerus lecontei, Scaphinotus bilobus, P. coracinus, S. inpunctatus, and C. ingratus.

Ants

We captured 11 species of ants, from 7 genera (Table 6). The most common species were Campanotus herculeanus and Myrmica brevinodis (38.8% and 39.3% of the total catch, respectively), found in all forest types and regions. We rarely captured Stenamma brevicorne, Leptothorax tricarinatus, Proformica limata, and Formica fusca fusca (Table 6), and each comprised less than 0.1% of the total catch.

Cluster analysis revealed no groupings by forest types or regions for ant communities. We found no difference in the total number of ants caught among the three regions, but four species were found in significantly different abundances in one region. M. brevinodis was significantly more abundant ($P < 0.001$) in the northwest, than in the other two regions (Table 6). F. f. marcida was significantly less abundant ($P < 0.001$) in Algonquin than in the northeast or the northwest. Acanthmyops interjectus was significantly more abundant in Algonquin than in the northeast, and not recorded in the northwest ($P < 0.05$).

We found no significant difference in the total catch of ants among forest types within each region, but when stands from all regions were pooled, our total catch of ants was significantly greater in the 'other' forest types than in pine forests ($P < 0.05$) (Table 6). Among individual species, four were significantly more abundant in the 'other' forest types compared to in pine forests: C. herculeanus and M. brevinodis ($P <$

0.001), and E. f. marcida, and A. interjectus ($P < 0.05$) (the latter species did not occur in the northwest). However, that result was reversed within the Algonquin region, and C. herculeanus, F. f. marcida, and M. brevinodis were more abundant in mature pine than in the 'other' forest type ($P < 0.05$). We recorded C. pennsylvanicus in only one pine stand, but found it in 'other' stands in all regions. Several infrequently captured species within each region were only found in one of the forest types for that region, but there was no consistency in forest selection among the regions by these rare species (Table 6). BDI ranged from 1.4 to 3.1 (Table 2, Figure 5) but we recorded no significant differences in diversity among regions or stand types.

There was a significant discriminant model among stand types (Wilks lambda = 0.68, $P = 0.02$), with C. herculeanus and F. f. marcida as the most important species. These two species were most abundant in 'other' forest in the two northern regions, but not in Algonquin. The model correctly classified the stands for old pine, mature pine, and 'other' for 38, 68, and 72% of the cases, respectively. We also found a significant discriminant model among regions (Wilks lambda = 0.57, $P = 0.001$). Important species in the model were: F. f. marcida, M. brevinodis, and C. pennsylvanicis. The ability of the model to discriminate was 71% for the northwest, 58% for the northeast, and 61% for Algonquin. F. f. marcida was rare in Algonquin and most common in the northeast. Myrmica brevinodis was extremely abundant in the northwest but much less in Algonquin, and C. pennsylvanicus was most common in the northeast (Table 6).

Salamanders

We caught an average of 3.63 salamanders/100 TN among four species: eastern red-backed salamander (Plethodon cinereus), two-lined salamander (Eurycea bislineata), blue-spotted salamander (Ambystoma laterale), and yellow-spotted salamander (Ambystoma maculatum). A large proportion of the catch was composed of P. cinereus (75%) and A. laterale (19%) (Table 7). Only the latter two species were captured in sufficient numbers to permit detailed analysis.

The difference in total captures among regions was considerable, and our catch in the northeast was significantly larger than from the northwest ($P < 0.01$) (Table 7). Pairwise comparisons revealed that P. cinereus was more abundant in the northeast and Algonquin than in the northwest ($P < 0.005$). We caught most A. laterale in the northwest, but there was no significant difference in abundance among regions (Table 7). Cluster analysis showed that the northwest stands clustered apart from those of the other two regions (Figure 6).

P. cinereus was the most abundant species in all forest types in the Algonquin and northeast regions, but we only recorded it in the 'other' forest type in the northwest. Wherever this species was present, it made up the largest proportion (59.2 to 100%) of the salamander community (Table 7). We found A. laterale in all stand types in the northwest region, where it was the only species recorded for both ages of pine, and formed 40.8% of the salamander community found in the 'other' forest type. We captured A. laterale only in the 'other' stand type in Algonquin, and only in old-growth pine in the northeast, where it comprised a small proportion of the salamander community (10.9 and 11.4%, respectively). A. maculatum were found only in the mature pine forests of the northeast, and E. bislineata were encountered only in the 'other' forest type (old-growth hemlock - tolerant hardwood) in Algonquin; few of the latter two species were captured.

We found that there was no difference in the total capture of salamanders in the three stand types, across regions ($P > 0.1$). However, pairwise comparisons showed a significant difference in salamander abundance among types within the northeast region. Old-growth pine stands in the northeast had a greater abundance of salamanders than mature pine stands ($P < 0.01$) or 'other' stands ($P < 0.005$). Abundance of salamanders in old-growth pine forests of the northeast was more than 6 times greater than in any stand type in the northwest (Table 7); and the abundance of salamanders in the 'other' forest type in Algonquin was more than 4 times greater than in the 'other' stands in the northeast and northwest, but neither result was significant (Table 7).

The diversity indices (BDI) were low because we only found 4 species of salamanders. BDI revealed no significant differences in diversity among regions or stand types (Table 2).

Winter-resident birds

We encountered atypical winter conditions in 1994-95 (mildest winter on record, with little snow, and no snow until late January) that allowed us no temporal replication of the plots, and a much later initial reading than we had anticipated. There was no bias between observers for total birds counted, numbers of each species seen, or number of species recorded ($P > 0.5$).

None of our analyses indicated any grouping of either individual species or avian communities by forest type, or age of pine stand (Table 8). Downy woodpecker was the only species for which there was a significant difference by habitat type; it was more abundant in our 25% pine group than in the 50% pine or 100% pine groups, with

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pine age classes pooled. There was no difference in downy woodpecker abundance between age classes of pine for 50 and 100% pine plots. Pooled data for finches, woodpeckers, Paridae and Certhidae, or cavity nesters revealed no significant differences among either the original habitat classes or the pooled habitats.

Discussion

Small mammals

The diversity of species found in pine forests in this study was similar to that reported in other studies in uncut conifer-dominated forests in Ontario for boreal and Great Lakes-St. Lawrence forests (Nagorsen and Peterson 1981, Martell 1983, Thompson 1986, Brooks and Reid 1992, Jones and Naylor 1993). No species was recorded during this study that was either extralimital (Dobbyn 1994), or not previously found in other forest types. Microtus chrotorrhinus had not been recorded on our study area in the northwest, but had been found in nearby Quetico Park (Dobbyn 1994). In a single season study, located in similar forests 100 km west of those reported here as northeast, Jones and Naylor (1993) found a diversity index of 2.73 compared to our mean of 2.55 for both seasons. In Algonquin Park, Brooks and Reid (1992) had diversity indices of 2.04 and 2.15 in pine stands (our calculations from their data), that were similar to our spring value and, like our spring value, substantially higher than indices during the fall. Brooks and Reid (1992) recorded substantial numbers of Napeozapus insignis in their study, whereas we found none. All other studies have reported that small mammal communities were dominated by Clethrionomys gapperi and Peromyscus maniculatus, as we found for all of our forest stands.

There was only limited support to reject the first two hypotheses, that small mammal communities in old-growth pine differ from those in other uncut old forest types, and that small mammal communities differ between age classes of pine. The discriminant models provided mediocre classification results that were based primarily on a few rare species. Given the high probability that rare species fluctuate depending on competition (e.g., Hoyle and Boonstra 1986, Hallett 1991), and the reduced probability of their capture in periods of high abundance of the more common species, we believe that small mammal communities were not different among the forest types. The small mammal communities in these forests are likely a subsample of the general regional species mix. We concluded that the remaining white pine dominated forests in Ontario do not support unique small mammal communities compared with other

forests of similar age. Jones and Naylor (1993) reached the same conclusion for white pine forests near Sault Ste. Marie. Our data suggested that there was a low degree of habitat specialization in forest small mammal species at the stand level, and that structuring of communities is more likely a function of specific habitat factors, or interactions among the species.

We recorded most of our M. chrotorrhinus in pine stands. However, Jones and Naylor (1993) reported it in all their habitat types. Specialized stand characteristics, beyond the scope of our study, may be important to this species, such as transition areas and surface rock (Tim et al. 1977, Naylor and Bendell 1983).

There was clear support to reject the third hypothesis, that small mammal community structure is similar throughout the province. The discriminant model picked three of the most common species, C. gapperi, P. maniculatus, and Sorex cinereus as key variables, suggesting a robust model based on relative abundances and on the lack of P. intermedius in Algonquin. Dobbyn (1994) also reported no P. intermedius in Algonquin Park. Population dynamics (as inferred from uterine scars/female and adult weights) also differed among the regional, indicating that subpopulations within the province operate independently. The inference that population dynamics varied within species across the province is further supported by the presence/absence of the more rare species among the regions, and as suggested by data from other studies. For example, we recorded no M. chrotorrhinus from the Algonquin region, as did Brooks and Reid (1992) in 1990-91. However, earlier data from Falls (1987) and Falls and Falls (1988) showed that this species was moderately common in 1982 and 1983. Similarly, we recorded no N. insignis from either the northeast or Algonquin, yet they were common in Algonquin in 1991 (Brooks and Reid 1993), and rare but present in the northeast in 1992 (Jones and Naylor 1993). We concluded that small mammals have different community structures and that populations of individual species function independently of each other in widely separated areas within the province.

Carabid beetles

None of the species of ground beetle trapped and identified in 1994 were extralimital (Lindroth 1961, 1963, 1965, 1968, 1969). Most of the species, including the dominant 6 species, were habitat generalists or forest generalists (Lindroth 1961, 1963, 1965, 1968, 1969, Niemela et al. 1993). Our diversity indices, species richness, and in some cases dominant species were similar to those reported in other studies in boreal forest types in Canada (Niemela et al. 1993, Duchesne and McAlpine 1993, Niemela et

al. 1994), although none of these studies was in old white pine forests.

We found little support the first two hypotheses, that carabid communities in pine-dominated stands differ from 'other' conifer dominated stands, or between age classes of pine. Only 2 species, C. ingratus and P. coracinus, were most abundant in mature pine, and only in the northeast (despite being present in both other regions). There is insufficient information on the ecology of these species to explain our observation. In Alberta, Niemela et al. (1993) found that distinctly different forest types (i.e., aspen vs. spruce/aspen forests) supported different carabid communities. The lack of contrasts between carabids from different forest types in our study indicated that white pine-dominated forests do not provide exclusive habitat for unique ground beetle communities within the Great Lakes-St. Lawrence forest.

Our third hypothesis, that communities differ across the province was well supported for carabid communities. The discriminant models resulted in high predictive power, and the robustness of these models was strengthened by the occurrence of some of the most common beetles that we sampled. Studies in Finland (Niemela et al. 1994) also showed broad regional distinctions in carabid community structure, and they attributed the observed differences to moisture regimes, temperature regimes, and broad differences in plant communities. These explanations may also apply equally well to our communities. For example, the northwest is significantly drier than the eastern areas of Ontario (Environment Canada 1993). However, limited information on the autecology of carabids precluded clear interpretation of the community results beyond the observed regional differences.

Ants

There are no studies of total ant species community diversity from northern coniferous forests of Canada. The number of ant species that we encountered (11) was relatively low compared with those from hardwood forests in Maryland, where Lynch (1981) found 52 species. However, our diversity values and the relative proportions of Camponotus species were the same as those from a study in northwestern Ontario (Sanders 1970). He found that C. herculeanus was most abundant, followed by C. novaboracensis and C. pennsylvanicus, with relative frequencies of 80:5:1, respectively. Sanders also observed M. brevinodis and F. fusca, in northwestern Ontario; unfortunately he did not report the subspecies of F. fusca. We found F. f. marcida but not F. f. fusca in the northwest. There is some evidence from several studies that certain ant species may structure their communities through competitive exclusion of other species (Culver 1974, Davidson 1977, Lynch 1981, Fellers 1987, Savolainen and

Vepsalainen 1988, Savolainen et al. 1989, Puntilla et al. 1994). One of the dominant species from those studies was F. rufa, which we recorded in two forest types; however, we observed no depletion of other species in its presence.

There was limited evidence to reject our first hypothesis that white pine-dominated forests contain ant communities similar to those in 'other' forest types. The abundance of ants was significantly greater in 'other' forest types than in pine forests. Further, several individual species differences were found among stand types within each region. However, there was no distinctly different community of ants in old-growth pine forests. The discriminant model classified 'other' stands correctly, but could not adequately distinguish old pine from mature pine or 'other' forests, indicating that while 'other' stands were distinct, old pine stands were not.

We found no evidence to reject the second null hypothesis, that ant community structure does not differ between mature and old-growth pine forests. The discriminant model could not classify old pine stands. Sanders (1970) found that the abundance of ants was greatest in the younger stands, and that overmature forests contained the lowest numbers of ants in a spruce-fir forest. He attributed those results to a greater abundance of nesting sites (stumps and logs) following logging in the young stands than in older uncut forests. However, Sanders postulated that carpenter ants may reproduce more successfully in mature stands, where large living trees provide more permanent nesting sites.

Punttila et. al. (1994) found that the abundance and diversity of ant communities were higher in young coniferous forests than in old-growth forests, but that some ant species were more abundant in old-growth forest than in younger forests, and absent from recently clearcut sites in Finland. They suggested that old-growth specialist species were affected detrimentally by forest management. Our study did not find a unique ant community in old-growth white pine forests, nor any individual species that was specifically found in this habitat type.

We observed limited support to reject the third hypothesis, that ant communities differ with respect to location in Ontario. There was a significant difference in the total catch among regions, but several species (M. brevinodis, F. f .marcida, A. interjectus, C. herculeanus and F. f. fusca) had different distributions and abundances in the province. The discriminant model separated most northwest sites from the others but misclassified many of the Algonquin and northeast sites. Lack of documentation on the ranges for these species precluded further comparisons, but our finding suggested that ant communities in similar habitat types differed depending on their location in the province.

<u>Salamanders</u>

There are few studies of habitat selection by terrestrial salamanders from northeastern North America. Most research on terrestrial woodland salamanders has been in the U.S.A., from the Pacific northwest (Bury 1983, Aubrey et al. 1988, Welsh and Lind 1988, Welsh 1990, Bury et al. 1991), and the southeast (Bennett et. al. 1980, Enge and Marion 1986, Petranka et al. 1993). Salamander abundance and community diversity from those areas were high compared to our results.

The diversity of salamander communities found in pine forests in our study was similar to values reported from New England (Burton and Likens 1975b, Pough et al. 1987). In the Hubbard Brook Ecosystem, Burton and Likens (1975a,b) found a terrestrial salamander community composed of 5 species, and dominated (93.5%) by P. cinereus. Our salamander communities were more diverse than those reported by Pough et. al. (1987) from upper New York. He recorded only 2 species of salamanders, P. cinereus (58% of the catch) and the terrestrial eft stage of the eastern newt (Notophthalmus viridescens).

We recorded no species that was beyond its known range, but P. cinereus was at the northern and western edge of its geographical distribution (Cook 1984). Although we recorded no efts of N. viridescens, all three of our study areas fell within the range of this species (Cook 1984). Burton and Likens (1975b) recorded relatively few N. viridescens in terrestrial habitats. We recorded E. bislineata only in the Algonquin region, but this corresponds to its known range (Cook 1984).

Our results suggested that the first null hypothesis, salamander communities do not differ between old-growth white pine stands and other old forest types, was invalid. In the northeast, old-growth pine forests had a significantly greater abundance of salamanders than the old 'other' (spruce-poplar) stands. Data from the northwest did not show the same trend as in the northeast, primarily because significantly fewer P. cinereus occurred there than in the other two regions. The data from our northeast study area contradicted results from New York (Pough et al. 1987) and South Carolina (Bennett et al. 1980), that suggested conifer forest types are not preferred by salamanders over hardwood forests. There are three factors from the American studies that differed from our study and that may have influenced their conclusions: 1) both U.S. studies surveyed communities in young managed second-growth stands, whereas our habitats were mature or old-growth tolerant hardwoods; 2) conifers in more southerly regions tended to be located on upper slopes and ridge tops, and presented colder, drier environments than the white pine-mixed forests and 'other' stands in our study; and 3) a significant proportion of the species reported in the U.S. studies require

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water bodies to complete a portion of the life cycle, whereas all of our species use ephemeral water for breeding. Therefore, the American results are not strictly comparable to our data.

We found limited evidence to reject our second null hypothesis, that salamander communities do not differ in abundance and diversity between old-growth and mature white pine forests. In the northeast, we recorded significantly more salamanders in old pine than in mature pine. Several studies in the western U.S.A. reported an increase in salamander abundance and diversity along a gradient of seral stages, with some species found almost exclusively in old-growth coniferous forests (Bury 1983, Ramotnik and Scott 1988, Aubrey et al. 1988, Welsh and Lind 1988, Corn and Bury 1991, Gilbert and Allwine 1991, Scott and Ramotnik 1992). The western U.S. studies suggested that an abundance of woody debris, and climatic conditions in the Pacific northwest associated with old-growth coniferous forests resulted in unique habitat types used by certain species of salamanders.

There was clear support to reject our third null hypothesis, that the abundance and diversity of salamander communities does not differ with respect to region in the province. This result occurred primarily because P. cinereus was rare in the northwest but common in the other two regions. In the northeast and Algonquin regions, significantly more total salamanders were recorded than in the northwest.

Although no old-growth pine forests were sampled in the Algonquin region, we found that pine forests there contained fewer P. cinereus than did old-growth hemlock - tolerant hardwood forests. In contrast, old-growth spruce - intolerant hardwood forest types in the northeast contained significantly fewer P. cinereus than did old-growth pine forests. We suggest, in agreement with Pough et al. (1987) and Bennett et al. (1980), that where tolerant hardwood forests are common, P. cinereus may be less abundant in coniferous forests. In our northeast study area where few stands of tolerant hardwoods stands were present, P. cinereus may favour long-lived and structurally complex coniferous stands over mixed-intolerant hardwood forest types.

Winter-resident birds

We believe that the abnormal conditions of the 1994-95 winter affected the reliability of our winter bird observations. First, the lack of temporal replication reduced the value of the data. Second, our late start in February undoubtedly influenced the number of seed-eaters observed because the pines had already shed most of their seed and only white spruce cones remained. In particular, the results for red crossbills (Loxia curvirostra) may have been affected because these birds prefer

pine seeds (Benkman 1987). Third, the exceptionally warm temperatures, with little snow, may have enabled birds to forage farther than normal from roost sites and to find food resources ordinarily covered by snow (seeds, fruits).

Little is known about the ecology of passerine birds in winter in northern North American forests. It is likely however, that within patch factors may be more important than between-patch factors when considering broad habitat categories with large areas in undisturbed conifer-dominated forests. We expected older stands to contain a number of features to which bark-gleaners and cavity-users would respond positively, and that pine would be a major factor because of the longevity of pine snags. For example, Pearson (1993) found that even within a fragmented landscape, some species were predicted best by stand characteristics than by landscape features. Many of the resident species may be generalists within the mature and old-growth age classes, and if within-stand features are sufficiently abundant then the communities are not closed systems (Virkkala 1991a). Further, high variability in communities is expected for resident birds, particularly for ephemeral species such as crossbills and grosbeaks (Virkkala 1991a,b). We concluded that our data were insufficient to test our hypothesis because of high variability and insufficient sampling as a result of extraordinary winter conditions. We can draw no specific conclusion with respect to the role of pine stands in the ecology of winter-resident birds.

General conclusions

In any study like this, criticism can be directed at the adequacy of the taxa chosen as study organisms. All of the groups that we studied were chosen as strong candidates to reject the null hypotheses, particularly the hypotheses with respect to the age of pine stand, because at least some species in each taxon may depend on structures that accumulate in old forests. We specifically chose species that would form as rigorous a test as possible of the null hypotheses, while using species for which there was some autecological information.

There was limited support to reject the first null hypothesis, that animal communities differed between old white pine and 'other' old forests (Table 9), and no individual species relied solely on old pine forests. There was also only limited support to suggest that old-growth pine maintains different animal communities than those in mature pine. Again, no individual species was found only in one age class or the other. Finally, all taxa clearly indicated that pine forests in different areas of Ontario have distinct regional faunas (Table 9).

Our data are not completely definitive because many other taxa could be different in different age classes, and knowledge of forest birds suggests that our results may be spurious. Also, it was beyond the scope of this study to assess productivity for species other than small mammals, so we cannot say whether any of the species aside from *P. maniculatus* or *C. gapperi* reproduce optimally in old white pine stands. However, based on our information, we cannot recommend that large tracts of old-growth white pine be maintained specifically for their distinct animal communities. Arguably, any species dependent on old-growth pine would be a small species, likely an insect, that would require small stands for survival. In that situation, paying attention to the distribution of stands in time and space would minimize the need to maintain vast tracts of old-growth forest specifically for a distinct animal community. It is apparent that white pine forests maintain distinct animal communities in different areas of Ontario. This fact has a clear management implication: white pine in the mature and old-growth age classes must be maintained in all areas of the province where it occurs (or has occurred historically), in order to maintain provincial biodiversity.

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Table 1. Mean abundance/100 trap nights and standard error (SE) of small mammals captured at three locations, and in three forest types, in Ontario, 1994.

Species	Season	Algonquin		Northeast			Northwest		
		Mature White Pine	Old-Growth Hemlock - Hardwood	Old-Growth White Pine	Mature White Pine	Old-Growth Poplar - Spruce	Old-Growth White Pine	Mature White Pine	Old-Growth Spruce - Fir Hardwood
Clethriomonys gapperi	Spring	3.33 (0.15)	1.11 (0.15)	2.00 (0.09)	1.23 (0.18)	2.50 (0.49)	3.56 (0.30)	2.22 (0.74)	3.56 (1.23)
	Fall	20.31 (3.53)	2.49 (0.20)	10.20 (1.40)	12.26 (1.29)	8.80 (1.38)	28.55 (5.33)	30.79 (4.58)	36.79 (5.91)
Peromyscus maniculatus	Spring	2.22 (0.46)	1.75 (0.59)	0.52 (0.25)	1.35 (0.35)	1.02 (0.09)	1.48 (0.51)	0.96 (0.18)	1.18 (0.52)
	Fall	4.27 (1.87)	4.35 (0.68)	1.94 (0.32)	1.75 (0.64)	2.59 (1.24)	8.06 (1.45)	10.75 (2.37)	5.50 (1.90)
Microtus pennsylvanicus	Spring	0	0	0	0	0	0	0	0
	Fall	0	0	0.15 (0.15)	0.21 (0.10)	0.10 (0.10)	0	0	0
Microtus chrotorrhinus	Spring	0	0	0.22 (0.09)	0.19 (0.08)	0	0.22 (0.14)	0	0
	Fall	0	0	0.43 (0.35)	0.21 (0.10)	0	0.76 (0.38)	0.07 (0.07)	0.07 (0.07)
Tamias striatus	Spring	0.05 (0.05)	0	0	0	0	0	0	0
	Fall	0	0.09 (0.09)	0	0	0	0	0	0
Blarina brevicauda	Spring	0	0	0	0	0	0	0	0.07 (0.07)
	Fall	0.16 (0.07)	0.09 (0.09)	0	0	0	0	0	0
Sorex cinereus	Spring	0.21 (0.16)	0	0.22 (0.09)	0.25 (0.12)	0.28 (0.18)	0.15 (0.09)	0.07 (0.07)	0
	Fall	0.05 (0.05)	0.18 (0.18)	3.54 (1.39)	2.20 (1.05)	1.39 (0.64)	2.56 (0.74)	1.12 (0.33)	0.53 (0.34)
Napeozapus insignis	Spring	0	0	0	0	0	0	0	0.30 (0.18)
	Fall	0	0	0	0	0	0	0	0.15 (0.15)
Phenacomys intermedius	Spring	0	0	0.07 (0.07)	0.31 (0.11)	0	0	0	0.07 (0.07)
	Fall	0	0	0.44 (0.21)	0.33 (0.12)	0.27 (0.09)	0.08 (0.08)	0	0.08 (0.08)

Table 2. Brillouin diversity indices for taxa sampled at three locations in three forest types, in Ontario, 1994-95.

Taxa	Algonquin		Northeast			Northwest		
	Mature White Pine	Old-Growth Hemlock - Hardwoods	Old-Growth White Pine	Mature White Pine	Old-Growth Poplar - Spruce	Old-Growth White Pine	Mature White Pine	Old-Growth Spruce - Fir Hardwood
Ants	3.1	1.4	1.8	2.5	2.7	1.7	2.1	2.3
Terrestrial Salamanders	1.0	1.8	1.3	1.2	1.0	1.0	1.0	1.9
Small Mammals (Spring)	2.1	2.0	2.2	3.3	2.1	2.0	1.8	1.9
Small Mammals (Fall)	1.4	2.1	2.3	1.8	2.2	1.8	1.7	1.3
Carabid Beetles	5.8	4.5	4.3	5	6	3.5	4.2	3.3
Resident Winter Birds	N/A	N/A	3.9	4.0	4.7	N/A	N/A	N/A

Table 3. Weights and number of uterine scars/adult female for red-backed voles (Clethrionomys gapperi) at three locations and three general forest types, spring and fall 1994.

| Location | Forest Type | Adult mean wt. (SE) (n) | | | | Mean scars /adult female (n) |
| | | Spring | | Fall | | |
		Male	Female	Male	Female	
Northwest	Old pine	27.0 (0.38) (35)	29.5 (0.86) (12)	22.9 (0.19) (75)	26.7 (0.57) (38)	7.3 (0.45) (33)
	Mature pine	26.0 (0.88) (16)	25.2 (0.33) (11)	23.3 (0.28) (73)	27.4 (0.54) (50)	8.2 (0.52) (43)
	Other forest	28.4 (0.63) (31)	29.1 (0.76) (12)	23.2 (0.18) (106)	26.3 (0.50) (41)	7.5 (0.44) (34)
Northeast	Old pine	24.3 (0.49) (18)	25.6 (0.50) (7)	22.6 (0.23) (24)	26.2 (0.79) (21)	6.1 (0.63) (16)
	Mature pine	24.1 (0.61) (11)	29.0 (2.08) (5)	22.6 (0.24) (30)	25.7 (0.58) (23)	6.4 (0.67) (14)
	Other forest	22.7 (0.30) (12)	24.2 (0.57) (5)	22.8 (0.45) (19)	24.5 (0.86) (11)	5.8 (1.05) (4)
Algonquin	Mature pine	24.4 (0.50) (31)	25.4 (0.40) (25)	23.0 (0.45) (30)	25.1 (0.41) (23)	6.4 (0.39) (23)
	Other forest	25.0 (0.32) (6)	25.5 (0.89) (5)	23.3 (0.33) (12)	23.4 (1.10) (2)	3.5 (0.31) (2)

Table 4. Weights and number of uterine scars/adult female for deer mice (Peromyscus maniculatus) at three locations and in three general forest types, spring and fall 1994.

| Location | Forest Type | Adult mean wt. (SE) (n) | | | | Mean scars /Adult female (n) |
| | | Spring | | Fall | | |
		Male	Female	Male	Female	
Northwest	Old Ppne	20.7 (0.37) (14)	21.4 (0.70) (5)	18.3 (0.34) (15)	17.8 (0.22) (14)	6.2 (0.63) (12)
	Mature pine	20.9 (0.66) (8)	23.8 (1)	18.4 (0.26) (34)	20.2 (1.88) (7)	5.6 (1.07) (5)
	Other forest	20.8 (0.56) (9)	20.9 (0.85) (6)	18.4 (0.30) (20)	17.7 (0.57) (2)	4.0 (1)
Northeast	Old pine	20.3 (0.40) (7)		18.6 (0.32) (12)	18.9 (0.72) (3)	7.5 (1.55) (2)
	Mature pine	20.6 (0.52) (13)	24.9 (1.21) (8)	18.4 (0.59) (9)	20.0 (1.44) (2)	5.5 (2.47) (2)
	Other forest	19.9 (0.65) (8)	20.9 (1)	18.9 (0.48) (9)	17.8 (0.32) (3)	6.5 (2.47) (2)
Algonquin	Mature pine	23.3 (0.35) (23)	22.7 (0.62) (15)	18.7 (0.26) (33)	20.1 (1.09) (8)	5.7 (0.88) (3)
	Other forest	20.5 (0.71) (13)	22.2 (0.54) (4)	18.3 (0.42) (10)	19.1 (0.47) (9)	3.0 (0.26) (6)

Table 5. Mean abundance/100 trap nights (SE) of carabid beetles captured at three locations in three forest types, in Ontario, 1994.

Species	Algonquin		Northeast			Northwest		
	Mature White Pine	Old-Growth Hemlock - Hardwoods	Old-Growth White Pine	Mature White Pine	Old-Growth Poplar - Spruce	Old-Growth White Pine	Mature White Pine	Old-Growth Spruce - Fir hardwood
Synucus impuncta	2.64 (0.57)	3.56 (1.72)	6.48 (1.57)	5.56 (1.58)	1.23 (0.33)	1.03 (0.44)	2.19 (0.41)	1.02 (0.37)
Calathus advena	0.65 (0.27)	0.41 (0.18)	1.05 (0.34)	1.22 (0.55)	0.35 (0.19)	0.75 (0.50)	0.71 (0.24)	0.33 (0.16)
Calathus gregaris	0.54 (0.28)	0.22 (0.17)	0.85 (0.23)	1.38 (0.56)	1.43 (0.06)	0.35 (0.22)	0.72 (0.26)	0.17 (0.09)
Calathus ingratus	0.16 (0.13)	0	2.57 (1.24)	1.15 (0.52)	0.35 (0.12)	0.07 (0.07)	0.06 (0.04)	0.04 (0.04)
Scaphinotus bilobus	0.28 (0.11)	0.58 (0.50)	0.72 (0.41)	0.33 (0.22)	1.78 (0.73)	4.45 (1.30)	4.47 (0.83)	4.08 (1.80)
Pterosticus coracinus	1.60 (0.47)	2.36 (1.00)	2.85 (0.79)	3.65 (0.79)	0.67 (0.20)	0.25 (0.16)	0.25 (0.17)	0.14 (0.10)
Pterosticus adstrictus	0.27 (0.16)	0.05 (0.05)	0.14 (0.08)	0.36 (0.23)	0.08 (0.08)	0.07 (0.07)	0.06 (0.04)	0.03 (0.03)
Pterosticus adoxus	0.43 (0.12)	0.38 (0.16)	0.10 (0.07)	0.37 (0.33)	0	0	0.12 (0.10)	0
Pterosticus pennslyvanicus	0.43 (0.17)	0	0.25 (0.11)	0.17 (0.10)	0.08 (0.08)	0.15 (0.14)	0.40 (0.18)	0.36 (0.14)
Agonum thoryei	0.16 (0.08)	0.06 (0.06)	0.03 (0.03)	0.10 (0.07)	0.07 (0.07)	0.07 (0.15)	0.27 (0.15)	0.08 (0.08)
Agonum retractum	0	0.34 (0.22)	0.03 (0.03)	0.19 (0.15)	0	0.15 (0.15)	0.38 (0.19)	0.22 (0.14)
Sphaerodaerus leconti	1.50 (0.50)	3.04 (0.73)	0.62 (0.24)	1.43 (1.43)	0.92 (0.49)	4.27 (2.04)	4.99 (2.26)	2.88 (0.62)

Table 6. Mean abundance/100 trap nights (SE) of woodland ants captured at three locations in three forest types, in Ontario, 1994.

Species	Algonquin		Northeast			Northwest		
	Mature White Pine	Old-Growth Hemlock - Hardwoods	Old-Growth White Pine	Mature White Pine	Old-Growth Poplar - Spruce	Old-Growth White Pine	Mature White Pine	Old-Growth Spruce - Fir Hardwood
Camponotus herculeanus	9.189 (11.06)	0.592 (1.02)	3.250 (1.96)	5.144 (7.12)	26.055 (13.85)	8.393 (3.04)	10.584 (7.04)	18.892 (6.64)
Camponotus novaborcensis	1.664 (2.84)	0.335 (0.58)	0.255 (0.57)	0.989 (1.98)	0.828 (0.80)	0	0.417 (0.66)	0
Camponotus pennsylvanicus	0	0.999 (1.73)	0	0.079 (0.16)	1.417 (2.45)	0	0	0.146 (0.36)
Myrmica brevinodis	7.640 (3.95)	1.149 (1.99)	7.640 (3.95)	7.621 (5.37)	12.768 (1.99)	21.944 (0.13)	21.423 (6.12)	17.600 (9.82)
Formica fusca marcida	0.070 (0.16)	0	0.070 (0.16)	0.707 (0.63)	5.557 (3.24)	0.446 (0.45)	1.025 (0.99)	2.384 (2.2.9)
Formica fusca fusca	0	0	0	0	0.809 (0)	0	0	0
Formica rufa	0	0	0	0	1.905 (2.85)	0	0.999 (2.08)	0
Acanthmyops interjectus	0.099 (0.22)	16.026 (27.76)	0.099 (0.22)	0	0.119 (0.21)	0	0	0
Proformica lima	0	0	0	0	0	0.446 (0)	0	0
Stenamma brevicorne	0.549 (0)	0	0.699 (0)	0	0	0	0	0
Leptothorax tricarinatus	0.420 (0)	0	0	0	0	0	0	0.476 (0)

Table 7. Mean abundance/100 trap nights (SE) of terrestrial salamanders captured at three locations in three forest types, in Ontario, 1994.

Species	Algonquin		Northeast			Northwest		
	Mature White Pine	Old-Growth Hemlock - Hardwood	Old-Growth White Pine	Mature White Pine	Old-Growth Poplar - Spruce	Old-Growth White Pine	Mature White Pine	Old-Growth Spruce - Fir Hardwood
Plethodon cinereus	0.215 (0.14)	0.702 (0.22)	1.103 (0.51)	0.437 (0.14)	0.124 (0.07)	0	0	0.151 (0.15)
Ambystoma laterale	0	0.107 (0.11)	0.142 (0.03)	0	0	0.084 (0.08)	0.246 (0.07)	0.104 (0.06)
Ambystoma maculatum	0	0	0	0.045 (0.05)	0	0	0	0
Eurycea bislineata	0	0.171 (0.11)	0	0	0	0	0	0
Total Salamanders	0.215 (0.14)	0.980 (0.39)	1.245 (0.54)	0.482 (0.17)	0.124 (0.07)	0.084 (0.08)	0.246 (0.07)	0.255 (0.14)

Table 8. Mean abundance of resident winter birds (SE) near Rushbrook Lake (northeastern region) in old pine and other forest types, in February, 1995. Percent refers to % pine in the stand.

Species	Spruce Mixed	Mature White Pine			Old-Growth White Pine		
		25%	50%	100%	25%	50%	100%
Piciodes pubescens (downy woodpecker)	2.60 (0.80)	3.25 (0.83)	2.25 (0.83)	1.00 (0.71)	4.67 (2.65)	1.25 (0.83)	2.50 (0.50)
Piciodes villosus (hairy woodpecker)	0.20 (0.40)	0	0.75 (0.83)	0.50 (0.87)	0.67 (0.47)	1.00 (0.71)	1.00 (1.00)
Piciodes arcticus (black-backed woodpecker)	0.20 (0.40)	0	0.25 (0.43)	0	0	0	0.25 (0.43)
Dryocopus pileatus (pileated woodpecker)	0	0	0	0	0	0	0.25 (0.43)
Sitta canadensis (red-breasted nuthatch)	1.00 (1.55)	1.25 (1.64)	1.00 (1.73)	0.50 (0.50)	0	3.00 (1.58)	2.00 (3.46)
Parus atricapillus (black-capped chickadee)	8.00 (6.23)	6.25 (4.38)	6.25 (4.38)	9.25 (3.63)	7.67 (4.50)	8.25 (6.53)	5.75 (2.49)
Parus hudsonicus (boreal chickadee)	0	0	0	0	0.67 (0.94)	0	0
Cyanocitta cristata (blue jay)	0.20 (0.40)	0	0.50 (0.50)	0.50 (0.50)	0.67 (0.94)	1.75 (1.48)	0
Perisoreus canadensis (gray jay)	1.00 (1.27)	1.50 (1.66)	1.00 (1.00)	0.50 (0.87)	1.67 (1.7)	0.25 (0.43)	0.50 (0.87)
Bonasa umbellus (ruffed grouse)	0.80 (1.17)	1.25 (0.43)	0.50 (0.50)	0.25 (0.43)	0.33 (0.47)	0	0.75 (0.43)
Loxia leucoptera (white-winged crossbill)	2.40 (3.88)	0	0	0	0.67 (0.94)	0	0
Loxia curvirostra (red crossbill)	0	0	0	0.50 (0.87)	0.67 (0.94)	0.25 (0.43)	0
Certhia americana (brown creeper)	1.00 (1.10)	0.75 (0.43)	0.25 (0.43)	0	0.67 (0.94)	0.50 (0.50)	0.25 (0.43)
Turdus migratorius (American robin)	2.40 (3.01)	0.50 (0.87)	1.50 (1.50)	3.75 (4.15)	5.67 (4.19)	0	2.25 (3.9)
Pinicola enucleator (pine grosbeak)	0.20 (0.40)	0	0	0	0.67 (0.94)	0	0.25 (0.43)
Carpodacus purpureus (purple finch)	0	0	0	0	0.33 (0.47)	0	0
Carduelis pinus (pine siskin)	0	0	2.00 (2.45)	0.25 (0.43)	0.33 (0.47)	2.50 (4.33)	0.25 (0.43)
Strix varia (barred owl)	0	0	0.25 (0.43)	0	0	0	0

Table 9. Summary of evident for the rejection of the three null hypotheses among the five study taxa. (no = null hypothesis not rejected, some = some species differences, but inconsistent among classes, strong = null hopothesis rejected)

Species	Old pine vs old other	Old vs mature pine	Location
Small mammals	No	No	Strong
Carabid beetles	No	Some	Strong
Ants	Some	No	Some
Salamanders	Some	Some	Strong
Winter birds	No	No	-
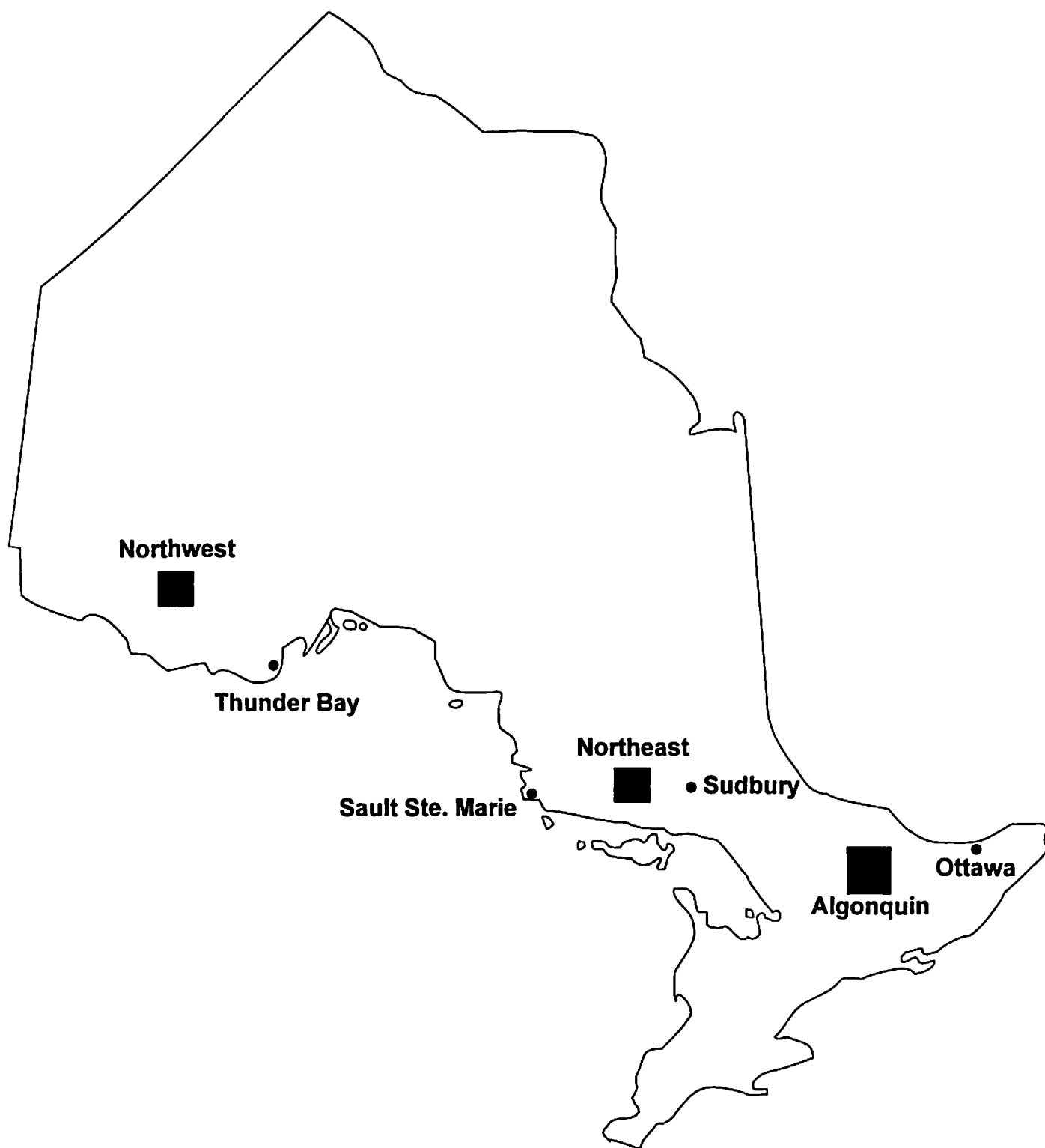
Figure 1. Location of the three study areas: northwestern Ontario, at White Otter Lake, northeastern Ontario, at Rushbrook Lake, and Algonquin, at Dacre, Whitney and Petawawa.
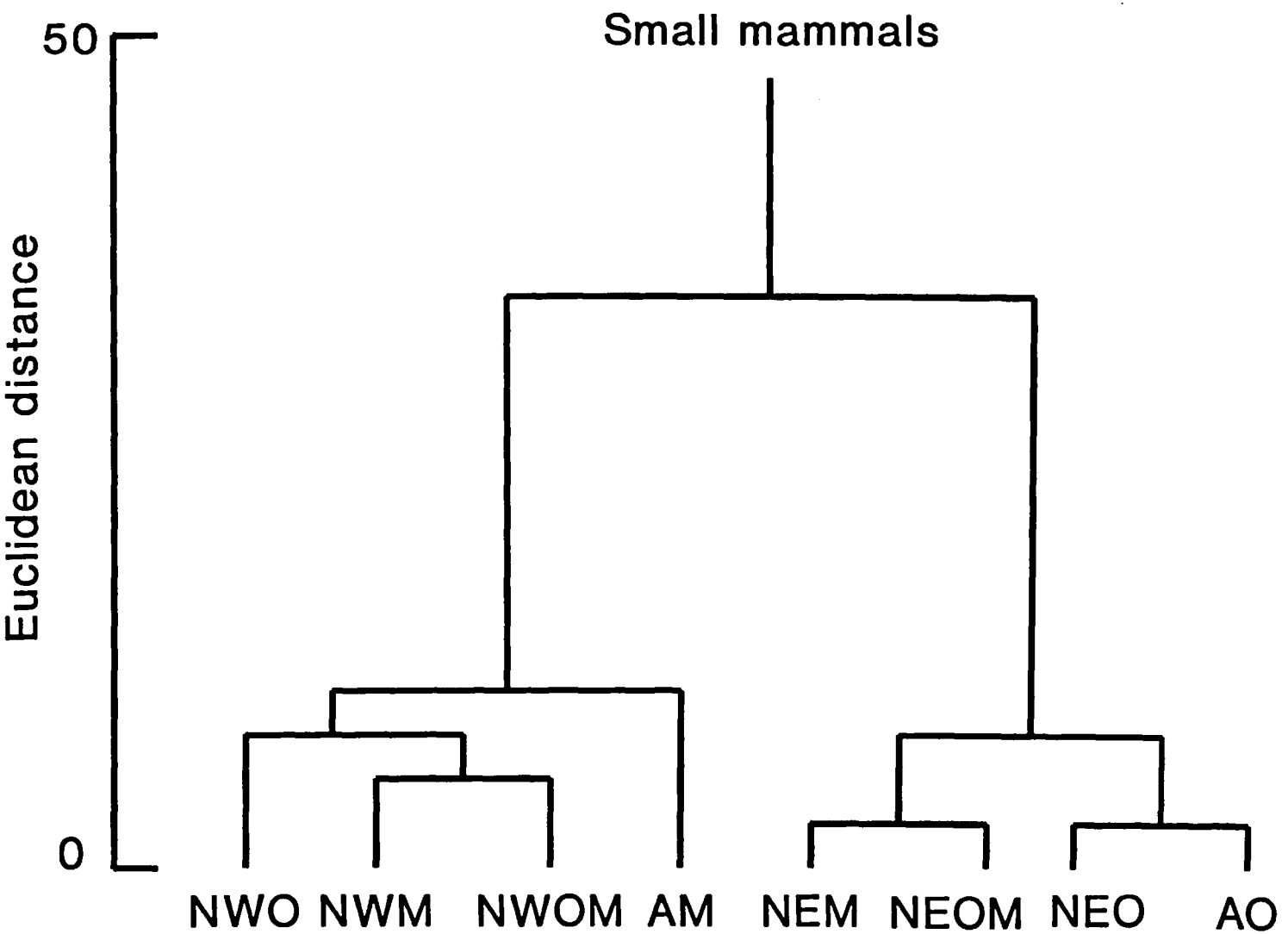
Figure 2. Cluster analysis for the small mammal community data in white pine and other mature forests in Ontario.

Legend: NW = northwestern; NE = northeastern; A = Algonquin OM = old growth (overmature); M = mature; O = other forest.
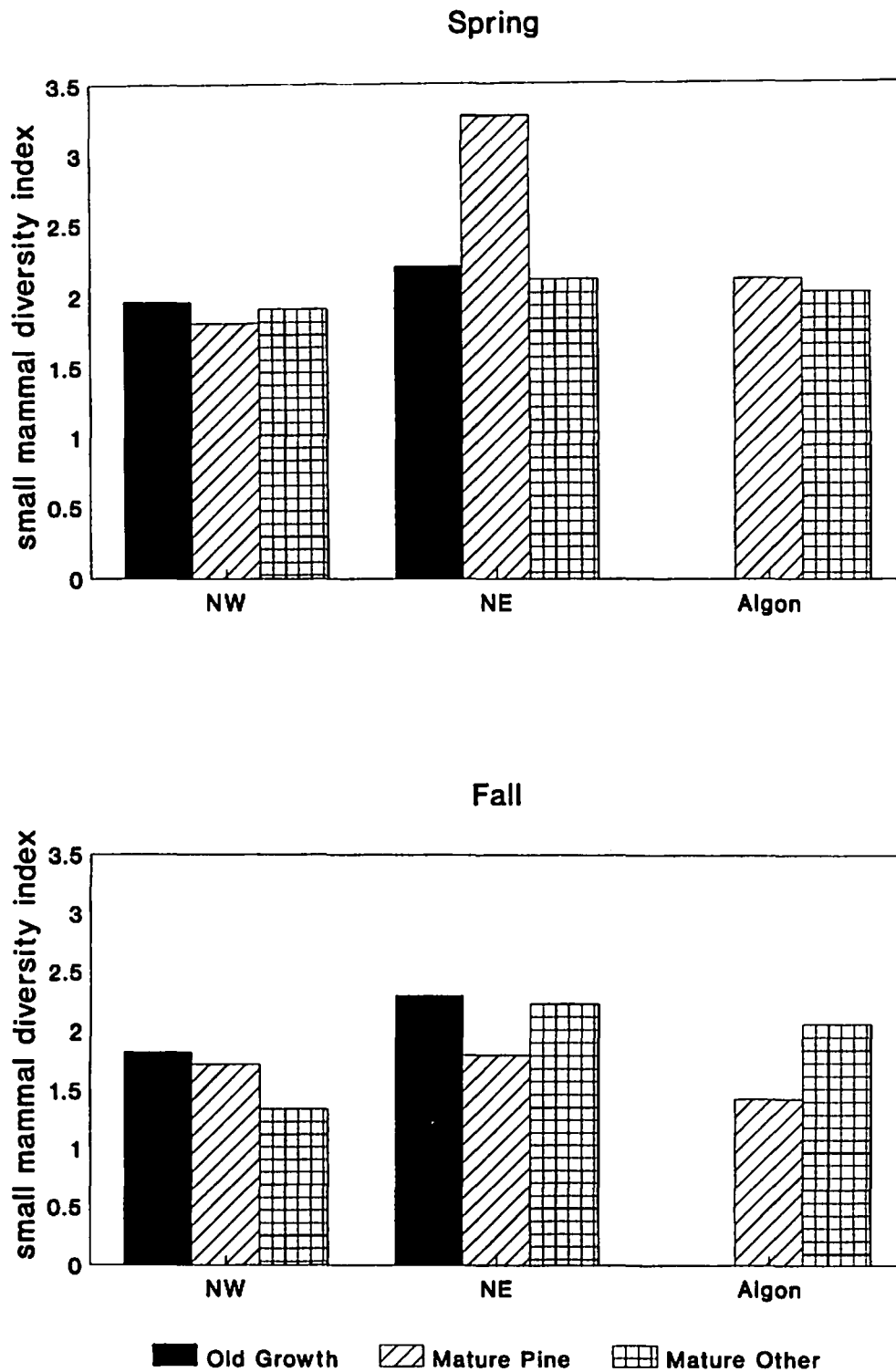
Spring

Fall

Figure 3. Brillouin diversity indices for small mammal communities in pine and other mature forests at three locations in Ontario.

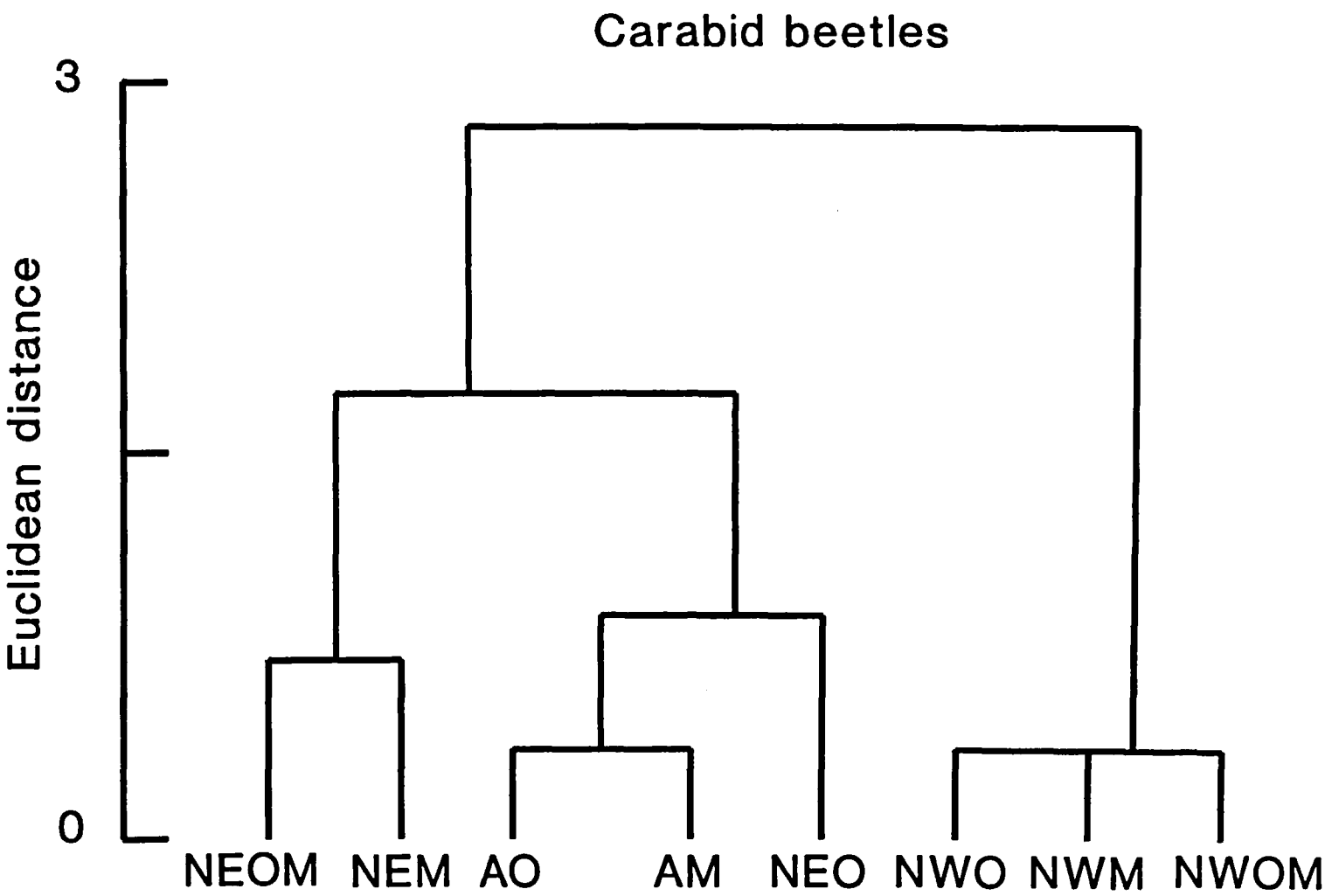Legend: NW = northwestern; NE = northeastern; A = Algonquin.

Figure 4. Cluster analysis of the carabid beetle community data in white pine and other mature forests at three locations in Ontario.

Legend: NW = northwestern; NE = northeastern; A = Algonquin
OM = old growth (overmature); M = mature; O = other forest.

Carabid beetles

Ants

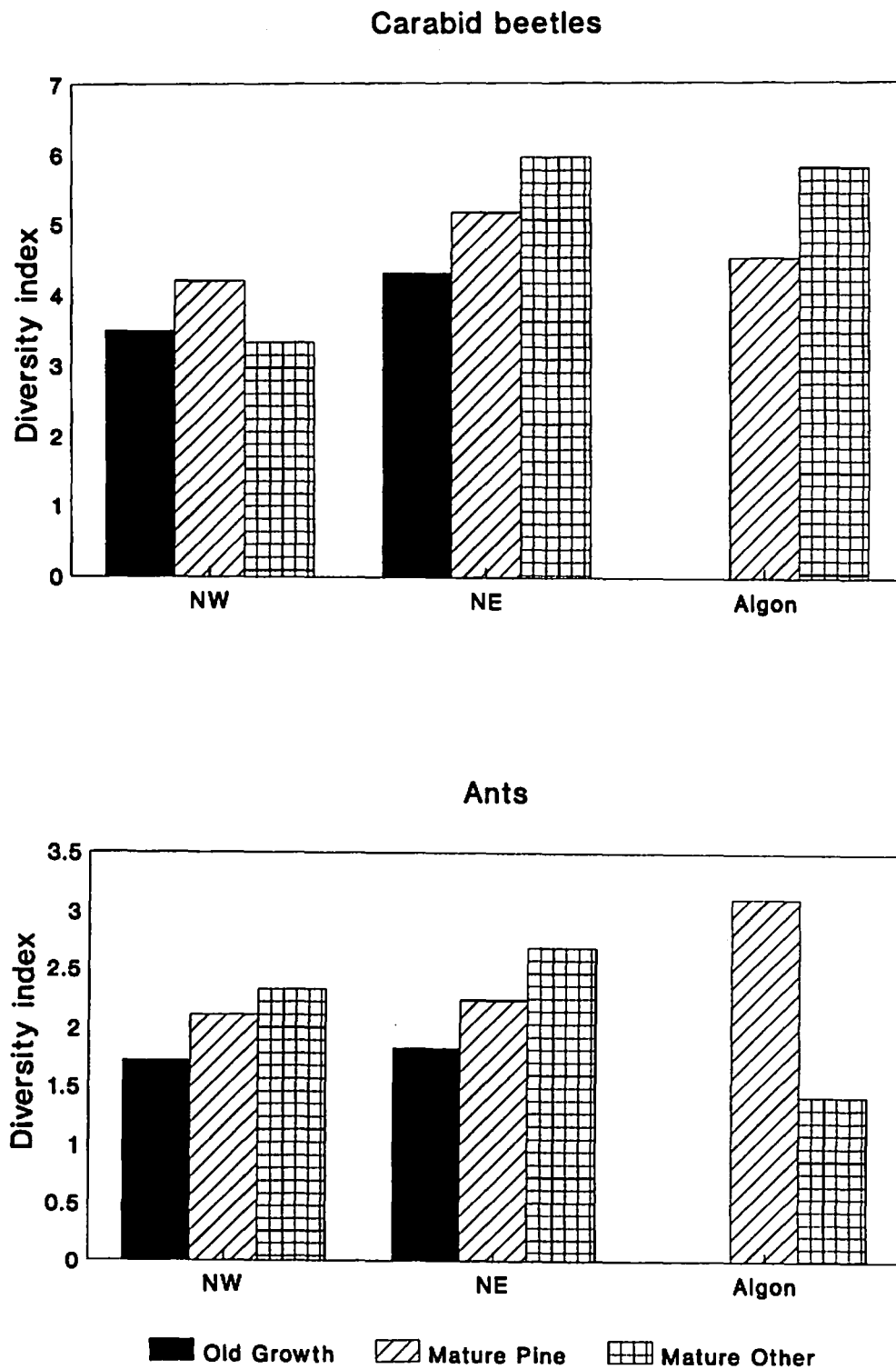Legend: ■ Old Growth ▨ Mature Pine ▦ Mature Other

Figure 5. Brillouin diversity indices for carabid beetle and ant communities in pine and other mature forests at three locations in Ontario.

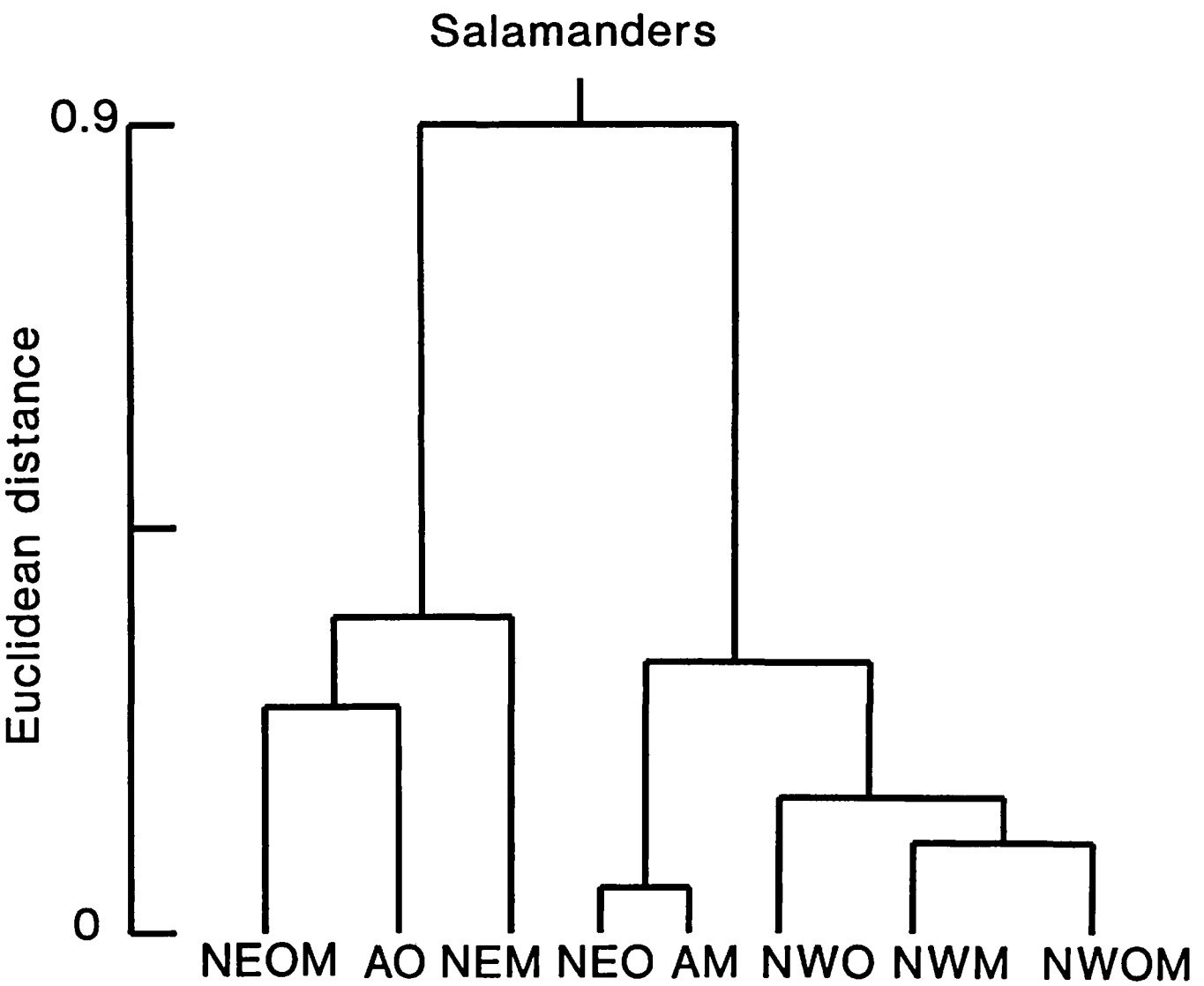Legend: NW = northwestern; NE = northeastern; A = Algonquin.

Figure 6. Cluster analysis of salamander community data in white pine and other forests at three locations in Ontario

Legend: NW = northwestern; NE = northeastern; A = Algonquin OM = old growth (overmature); M = mature; O = other forest.

Forest Landscape Ecology Program

1. **Development of a Spatial Data Base of Red and White Pine Old-growth Forest in Ontario (East).**
S. Pala (Spectranalysis Inc., Oakville, Ontario), 1992, 31pp.

2. **Understanding Old-growth Red and White Pine Dominated Forests in Ontario.**
T.J. Carleton (Faculty of Forestry and Department of Botany, University of Toronto) and A.M. Gordon (Department of Environmental Biology, University of Guelph), 1992, 76pp.

2A. **Understanding Old-growth Red and White Pine Dominated Forests in Ontario.**
Appendices.
T.J. Carleton (Faculty of Forestry and Department of Botany, University of Toronto) and A.M. Gordon (Department of Environmental Biology, University of Guelph), 1992, 215pp.

3. **Fauna of Red and White Pine Old-growth Forests in Ontario.**
Issues and Recommendations for Research.
D.A. Welsh (Canadian Wildlife Service, Nepean, Ontario), T. Clark (CMC Consulting, Bracebridge, Ontario) and K. Clark (Biota Environmental Consulting, Dorset, Ontario), 1992, 56pp.

4. **Scenic Beauty and other Values of Red and White Pine Old-growth Forests.**
W. Haider (Centre for Northern Forest Ecosystems Research, Fisheries and Tourism Research Unit, Lakehead University), 1992, 145pp.

5. **Development of a Spatial Data Base of Red and White Pine Old-growth Forests in Ontario - (West).**
S. Pala (Spectranalysis Inc., Oakville, Ontario), 1992, 42pp. & App.

6. **A Computer Program for Landscape Diversity Analysis: LDA Version 2.0 -**
- (A User's Manual).
A.H. Perera and F. Schnekenburger (Ontario Forest Research Institute, Ontario Ministry of Natural Resources), 1993, 25pp. & App.

7. **A Pilot Landscape Ecological Model for Forests in Central Ontario.**
L.E. Band (Department of Geography, University of Toronto, Ontario), 1993, 40pp.

8. **Early Successional Processes of Eastern White Pine and Red Pine in the Great Lakes - St. Lawrence Forest.**
H.M. Kershaw (Devlin Consulting Services, Sudbury, Ontario), 1993, 50pp.

9. **Spatial Characteristics of Eastern White Pine and Red Pine Forests in Ontario.**
A.H. Perera and D.J.B. Baldwin (Ontario Forest Research Institute, Ontario Ministry of Natural Resources), 1993, 82pp. & App.

10. **Natural Establishment and Early Growth of Eastern White Pine in the Great Lakes**
- St. Lawrence Forest: An Annotated Bibliography.
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