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Comparison of habitat characteristics of second- and old-growth forests of the Temagami region of northern Ontario and their relationship to bird abundance.

by

Jill A. Jensen

Thesis submitted to the School of Graduate Studies and Research, University of Ottawa, in partial fulfillment of the requirements for the M.Sc. degree in the

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Ottawa, Ontario, Canada

March, 1993

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ACKNOWLEDGEMENTS

I would like to thank my supervisors David Currie and Scott Findlay for their guidance, great ideas, always making time in their busy schedules and for putting up with my failure to accept the philosophy of statistics. Also, my supervisory committee Gray Merriam, and Dan Welsh, for his wealth of knowledge about birds and forestry which kept me on track and for keeping me challenged.

I sometimes wonder how I would have made it through my first field season without Peter Quinby's help, advice and talent for scamming. Peter found me a canoe (thanks to Hap Wilson), loaned me equipment, taught me how to identify vegetation, introduced me to Rusty Nails (and rusty nails) and gave me some very helpful advice. He also throws great field parties. I would also like to thank Peter and Marie for feeding me real food on occassion and providing a haven in a July 1st snowstorm.

Thanks to my hard-working field assistants, David Gravelle and Dominique Arranz for donating a lot of sweat and blood (to blackflies and mosquitoes). Also, Ian and Lianne for shelter, dinners, videos and fun. And to the best field-crew in the world: Mike, Brian and Paul (who among other talents can build a sauna in the middle of nowhere) and of course, Leslie and Landis who helped me immeasurably in the field but most importantly are great friends, kindred spirits and SO MUCH FUN!

Earthwatch volunteers also helped with vegetation sampling and moral support. Thanks particularly to Hana Heger who paddled and portaged two days for my research.

Andrea, Rich and Chris listened to me whine alot and taught me lots about birds. Thanks for helping with CANOCO Chris- even if I did decide against it. Thanks to Lisa Venier and Heather Dewar (nearest-neighbour programs-yuk!) for their support. To Connie and Monica- who could be so lucky as to have friends who'll listen to bird tapes with them? Thanks you two- for bird discussions, stats chats and well... for just about everything. And to all my other friends who didn't abandon me even if I did become a social recluse.

And thanks of course to my fellow grad students especially the Penthouse gang, and most especially, Pam, Iain, Aspa, Mike and Paul, for dinners, incredible support- emotionally and intellectually, friendship and for making the whole experience unforgettable. Thanks as well to Alain Filion for translating my abstract.

And last but certainly not least, I'd like to thank my family for their support and interest.

Financial support for this study was provided through an NSERC grant.

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ABSTRACT

Logging influences the distribution and abundance of breeding birds by changing the structure and composition of forests. In particular, very little old-growth forest remains. Studies suggest that the structural characteristics of old-growth forests of the Pacific North-west provide habitat not available in younger forests.

This study compared certain characteristics of habitat structure, and abundance of selected bird species in three forest types in the Temagami region of northern Ontario: (i) old-growth pine forests (no history of catastrophic disturbance) (ii) mature pine forests (undisturbed for approx. 100 years) (iii) managed forests (previously pine-dominated and selectively-logged approx. 50 years ago).

Canopy height, tree species diversity and percent cover of vegetation in the upper canopy, average number of vegetation layers and spatial variability in the number of layers were all significantly greater in old-growth that in managed or mature forests. Abundances of some bird species were significantly correlated with habitat characteristics. However, none of the bird species censused were significantly more abundant solely in old-growth forests. Our results suggest that vegetation characteristics predict bird abundance more strongly than forest type.

RÉSUMÉ

En modifiant la structure et la composition des forêts, les coupes forestières influencent la distribution et l'abondance des oiseaux nicheurs. Plus particulièrement, il ne reste maintenant que très peu de forêts anciennes. Certaines études suggèrent que les caractéristiques physiques des forêts anciennes de la côte ouest de l'Amérique du Nord fournissent des habitats fauniques qui ne sont pas disponibles dans des forêts plus jeunes.

Dans cette étude, nous comparons certaines caractéristiques de la structure de l'habitat et l'abondance de plusieurs espèces d'oiseaux dans trois types de forêts de la région de Témagami, Ontario: (i) forêts anciennes de pins (sans histoire de perturbations catastrophiques), (ii) forêts matures de pins (sans perturbations depuis environ 100 ans), et (iii) forêts exploitées (forêts de pins à l'origine, puis coupées sélectivement il y a environ 50 ans).

La hauteur de la voûte du feuillage, la diversité spécifique des arbres, le pourcentage de recouvrement de la végétation au niveau de la voûte du feuillage, le nombre moyen de strates de végétation et la variabilité spatiale dans le nombre de strates étaient tous significativement plus élevés dans les forêts anciennes que dans les forêts matures ou les forêts exploitées. L'abondance de certaines espèces d'oiseaux s'est avérée significativement corrélée avec les caractéristiques structurales de la voûte du feuillage. Toutefois, aucune des espèces d'oiseaux recensées n'était significativement plus abondante uniquement dans les forêts anciennes. Nos résultats suggèrent que les traits structuraux des forêts anciennes de pins ne semblent pas procurer des habitats qui ne seraient pas disponibles dans les forêts matures ou exploitées. D'ailleurs, l'abondance des oiseaux est mieux prédite selon les caractéristiques de la végétation que selon le type de forêt.

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GENERAL INTRODUCTION

Forests have been altered significantly by human activities in the last century. There are three primary causes. The first is intensive cutting, usually of the largest (oldest), most commercially valuable trees. The second is the tendency to manage forests on short-rotational cutting cycles, thereby truncating the developmental life-cycle of the forest. The third, is the successful control of fire in recent decades which has inhibited regeneration of certain tree species.

Recently, there has been increased public concern over the management of forest resources. Much of this concern has focused on the conservation of old, undisturbed (i.e. old-growth) forests. This stems partly from the rarity of some old-growth ecosystems. For example, the extent of such forests in the Douglas-fir (*Pseudotsuga menziesii*) region of the Pacific Northwest was estimated at approximately 6 million hectares at the time of European settlement. Only 2 million hectares remain, 80 percent of which is unreserved and potentially available for logging (Barnes, 1989; Spies and Franklin, 1988).

Old-growth forests are highly valued by the public. For some, the value of old, undisturbed forests derives from their inherent aesthetic, wilderness and spiritual values. Wilderness is also economically important to recreation and tourism industries. Old-growth forests are also a natural scientific laboratory and provide, as Leopold (1970) describes, "a base datum of normality". Others value the economic importance of harvesting old-growth since old-growth forests are a valuable source of timber. The economy of many communities is strongly dependent on the logging industry.

Studies of old-growth Douglas-fir forests have demonstrated their ecological importance. These forests differ in structure from younger forests. Old-growth Douglas-fir forests have significantly higher densities of large trees and snags, a taller canopy, greater tree-size variability and greater vertical diversity than younger forests (Spies and Franklin, 1991; Bingham and Sawyer, 1991; Carey *et al.*, 1991; Huff *et al.*, 1991). These structural characteristics provide important habitat for some wildlife species (e.g. Carey, 1989; Mills *et al.*, 1991; Lundquist and Mariani, 1991).

Unfortunately, most ecological arguments for the conservation of old-growth forests are based on studies in the north-western United States and little is known of the ecology of other old-growth forests. Forest ecosystems differ in their life-cycle, climatic conditions, fire ecology and associated wildlife species. Effective management decisions will require information on the ecology of all types of old-growth forest.

This study focuses on the ecology of eastern old-growth pine forests in the Temagami region of Ontario. At the turn of the century, the Temagami region was considered to be the best pinery in central Canada (Hodgins and Benedickson, 1989). A survey conducted in the early 1900's estimated some 410,000 hectares of pine forest in the region (Hodgins and Benedickson, 1989). These extensive forests of White (Pinus strobus) and Red Pine (Pinus resinosa) attracted commercial interests as early as the 1890's (Hodgins and Benedickson, 1989), and by 1980, the amount of White Pine forest had declined to 14,000 hectares (Benson, 1990). Despite intensive logging, some large areas of undisturbed forests still remain. The old-growth pine forest of the Wakimika Triangle region of Temagami is possibly the largest continuous stand of old-growth White Pine remaining in Ontario (Pinto, 1989). Ontario's old-growth red and white pine forests are disappearing at a rapid rate- proposed harvesting could eliminate some of the last remaining old-growth forest ecosystems (OMNR, 1993).

Historically, Temagami has been a region of multiple use: timber extraction and mining have been the foundation of the region's economic development, as have summer camps and tourism, particularly angling, hunting and recreational canoeing. However, in the early 1980's, plans to log old-growth stands generated intense conflict among user-groups. Protesters blockaded logging roads and many citizens, including a future premier of Ontario, were arrested in attempts to protect Temagami's old-growth forests.

In 1992, the provincial government established the Old Growth Conservation Initiative with a mandate to develop recommendations for management of Ontario's old-growth forests. One recommendation was for further ecological research to determine how old-growth forests differ from other forests in diversity, structure and importance of habitat (OMNR, 1993). Despite their importance, no studies on the ecology of Temagami's old-growth pine forests have been published in the scientific literature.

The intent of this study is two-fold. The first chapter compares the structure and diversity of vegetation in old-growth, mature and managed forests. The second chapter compares the abundance of selected bird species in these same forest stands, and relates species abundances to habitat characteristics.

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CHAPTER 1

Structural Characteristics of Second- and Old-Growth Forests in the Temagami Region of northern Ontario.

ABSTRACT

Old-growth Douglas-fir (*Pseudotsuga menziesii*) forests of the Pacific North-west have been shown to differ structurally from younger forests; old-growth forests had significantly higher densities of large trees and snags, higher canopies, greater tree size variability and greater vertical diversity.

In this study we compare the structure and composition of vegetation in old-growth pine forests (no history of catastrophic disturbance for at least 150 years), mature pine forests (undisturbed for approximately 100 years) and managed forests (previously pine-dominated and selectively-cut roughly 50 years ago) in the Temagami region of northern Ontario. Eastern old-growth pine forests did not differ from mature and managed stands in the densities of large trees or species diversity of trees and shrubs. Large snag density was significantly higher in old-growth than mature stands. Managed stands did not differ from the other forest types in large snag density. Canopy height, number of tree species and percent cover of vegetation in the upper canopy, average number of vegetation layers, and spatial variability in the number of layers were all significantly greater in old-growth than in mature or managed stands. However, although statistically significant, differences in canopy-related characteristics among forest types were not strong. We conclude that insofar as conservation of these structural

characteristics is a management goal, forest-type is a poor criterion for preservation.

INTRODUCTION

The life-cycle of a forest can be classified into three stages: young, mature and old-growth (Thomas *et al.*, 1988). Young forests grow quickly, and reach the mature stage when the rate of wood production of the dominant trees begins to decline. With advancing age, the rate of wood production declines further and older trees begin to rot and die.

In the past decade, increasing concern over forest management practices has centred largely on the disposition of old-growth forests. Aside from their economic value for timber, these forests are highly valued for recreation, and their inherent aesthetic qualities. Some old-growth forest ecosystems appear threatened. For example, the coniferous forests of the Pacific Northwest and Ontario's old-growth pine forests are being harvested at a rate which exceeds their replacement rate (Franklin *et al.*, 1981; OMNR, 1993). This raises the concern that these communities, which may possess important features (such as unique species), will be eliminated.

Most research on old-growth forests has been conducted in old-growth forests of the Pacific Northwest. In what has been viewed as a landmark paper, Franklin et *al.* (1981) define old-growth forests as ecosystems that have developed over a long period essentially free of catastrophic disturbance. They conclude that most of the distinctive features of old-growth Douglas-fir (*Pseudotsuga* *menziesii*) forests can be related to structure: large, live trees, large snags, and large logs (on land and in streams). They also conclude that the structure of old-growth forests is more heterogenous than that of younger forests.

This initial research, however, was largely descriptive. Franklin *et al.* (1981) presented no data to support the conclusion that old-growth forests have higher densities of large trees than other forest types. There were no statistical comparisons of large log densities, and natural young Douglas-fir stands surveyed at the same time as old-growth had masses of logs as large as found in some old-growth stands. The mean diameter of snags increased from stand ages 35 to 200 years (Cline *et al.*, 1980) yet there is no comparison of old-growth forests, as a group, to other forest types. The data used to compare the heterogeneity of old-growth to younger forests showed no statistically significant differences "due to a small and unequal sample size." They state further that "there are few data to support the intuitive prediction that the spatial heterogeneity of old-growth is greater than that of young-growth."

These unsubstantiated descriptors of old-growth forests have been frequently cited (e.g. Meslow *et al.*, 1981; Whitney, 1987; Spies, 1990). White (1990) likewise uses a similar set of features to characterize old-growth in eastern Ontario, based on research by Parker (1989), Hunter

(1989) and Barnes (1989); all qualitative studies. Martin (1992) similarly describes old-growth mixed mesophytic forests of the southern Appalachians and Tomialojc (1991), old-growth forests of Poland, again without comparison to younger forests.

More recent studies, again in the Pacific Northwest, have compared old-growth stands to mature and young forest stands in terms of their structural characteristics. The characteristics found to distinguish old-growth from younger forests were similar to those identified in earlier studies. Old-growth Douglas fir forests had significantly higher densities of large trees and snags, a taller canopy, greater tree-size variability and greater vertical diversity than younger forests (Table 1). These structural characteristics may provide important wildlife habitat (for example, James and Wamer, 1982; Mannan *et al.*, Mills *et al.*, 1993). There were few examples of plants that were restricted to, or found optimal habitat in old-growth Douglas-fir forests (Spies, 1991).

Old-growth forests of other regions may have similar characteristics. Similar structural changes occur along a developmental continuum in all forests (i.e. increase in tree girth and height, death of old trees, increased tree-size variability). However, forest ecosystems vary in vegetation-type, average life-span of dominant trees, climate, growth rate and fire ecology, all of which influence vegetation structure.

Unfortunately, few data exist on the structure of old-growth forests outside the Pacific North-west. Moreover, the distinguishing structural features of western old-growth forests have often been applied to describe the structure of old-growth forest ecosystems elsewhere. This type of universal categorization is not appropriate when in practice, forest management is conducted on a regional scale. To make effective management decisions regarding old-growth forests, regional information is necessary.

Large areas of undisturbed pine forest remain in the Temagami region of northern Ontario. Plans to manage these forests are controversial. The implications of harvesting remaining old-growth stands will depend in part on the degree to which these forests constitute distinct habitats. Quinby (1989) described the structural features of these forests, but no study has compared the features of these old-growth stands to second-growth forests.

In this study we determine if old-growth pine forests, mature pine forests and managed forests of the Temagami region can be distinguished in their structure and diversity of vegetation.

ECOLOGY OF PINE FORESTS

i. General ecology

In their natural state, concentrated stands of red and white pine are rare. Red and white pine are generally found in mixed-wood stands with 30 to 60 percent hardwoods (OMNR, 1993). Red pine can grow up to 350 years of age, with the average height at maturity about 25 meters. Red pine grows best on deep, well-drained fine sands and loams. It is considered very sensitive to competition from other plants and, being relatively intolerant to shade, requires full sunlight for optimal seedling growth (OMNR, 1993). White pine can grow to 500 years of age and will commonly attain heights of 30 meters. It grows best on fine sandy loams and regenerates best in the partial shade of other trees (OMNR, 1993).

ii. Geographical range

The range of white pine extends from Newfoundland to Manitoba, south through the northern United States to Pennsylvania, northern Ohio, and southeastern Iowa, and southward along the Appalachian Mountains to northern Georgia (Grimm, 1983). Red pine extends from Nova Scotia westward to Manitoba and south to Minnesota, Michigan, Pennsylvania, and Massachusetts (Grimm, 1983). In Ontario, this range generally encompasses the Great Lakes-St Lawrence forest region. According to Morse (1984), red and white pine were the dominant trees in Ontario when European settlers first arrived.

iii. The role of disturbance in pine ecosystems

Pine forests are generally thought to develop following intense fires (Graham, 1941; Maissurow, 1941; Hough and Forbes, 1943; Chapman, 1947) which create a receptive seedbed and reduce competition from other vegetation (Maissurow, 1935; 1941). Red and white pine are well-adapted to surviving "non-catastrophic" fire (i.e. surface fires of light to moderate intensity); their thick bark enables them to resist fire that doesn't affect the living crown (Hare, 1965; Van Wagner, 1971).

Prior to fire suppression, red and white pine were favoured by non-catastrophic fires occurring at intervals of 20 to 40 years combined with more intense fires on a 150 to 200-year cycle that would kill most trees (Cwynar, 1977). Pine regeneration also depends on the creation of canopy gaps (Hibbs, 1982). Canopy gaps are created by windstorms or the death of canopy trees which enables germination of new individuals.

iv. Succession

Nichols (1935) compared the hemlock-white pine-northern hardwood community to the position occupied by Douglas fir in the Pacific Northwest in relation to the "climatic-climax" of the region. The succession of red and white pine is not well understood (OMNR, 1993). The structural variability found in old pine stands suggest that there are multiple pathways leading to this phase (Carleton and Gordon, 1992); many factors influence succession including forest composition, forest floor conditions, soil condition and fire frequency and intensity (Struik,1990; Steill, 1978; Van Wagner, 1971; Quinby, 1988; 1991).

Day and Carter (1991) suggest that in the absence of catastrophic fire, pine forests may be replaced by shade-tolerant species such as balsam fir, cedar, red maple, white birch and mountain maple. Others claim that continuous white pine recruitment occurs within old-growth white pine-dominated stands (Gilbert, 1978; Holla and Knowles, 1988; Quinby, 1989). This continuous recruitment of white pine may take place for centuries in response to non-catastrophic disturbance resulting in an uneven-aged stand structure (Quinby, 1991).

Table 1 - Summary of results of studies conducted in the north-western United States comparing vegetation characteristics of old-growth, mature and young Douglas-fir forest stands.

LOCATION	RESULTS	TEST	REFERENCE
Oregon and Washington	Density of large trees and variability in tree size discriminate best among age-classes	Discriminant Analysis	Spies and Franklin, 1991
Oregon and California	Basal areas of large and tall trees discriminate best among age classes	Discriminant Analysis	Bingham and Sawyer, 1991
Oregon	Density of large conifers and snags, canopy height and vertical diversity of conifers positively correlated with stand age	Pearson or rank correlations	Carey *et al.*, 1991
Washington	Density of large trees and snags, and total log volume higher in old-growth than mature stands	Mann-Whitney U-test	Huff *et al.*, 1991

METHODS

STUDY AREA

Study sites were located in the Temagami region of northern Ontario between approximately 46°50'N, in the south-west arm of Lake Temagami, and 47°08'N at the north end of Lake Obabika. The study area ranged west to 81°21'W, on the Obakika River and east to 79°36'W on Rabbit Lake (Fig. 1).

Brown *et al.* (1980) described the climate of the region. Mean temperatures range from -13°C in January, to +19°C in July. Annual precipitation is approximately 800 mm, and annual actual evapotranspiration is approximately 600 mm (UNESCO, 1977).

The topography of the Temagami region ranges from rolling hills to steep cliffs. The Ishpatina Ridge, at 1000 meters, is the highest point in Ontario. Soil depths vary, with exposed bedrock or shallow soils in upland areas. Soils are generally glacial tills, mostly dry to moist silty loams (Johnson, 1988). Gravels and sands of glaciofluvial origin occur in valley bottoms (Johnson, 1988). Sandy beaches are found on many of the larger lakes.

The region of Temagami lies in the transition zone between the Great Lakes-St. Lawrence forest and the more northern Boreal forest (Rowe, 1972). Rowe (1972) describes the region:

"The typical association of the section consists of

> eastern white pine with scattered white birch and white spruce, although the spruce frequently rivals the pine in abundance. Another common, though variable type is a mixture of birch, pine and spruce, with balsam fir, trembling and large-toothed aspens. Both red pine and jack pine are present, the former often prominent in bluffs along ridges and the latter generally restricted to the driest sandy or rocky sites. The tolerant hardwoods, yellow birch and sugar maple, have only a scattered occurrence. The prevalent forest cover on the uplands is clearly a reflection of periodic past fires, and the sandy soils have provided conditions especially favourable for the propagation of eastern white pine, red pine and jack pine. On the lowlands, in poorly-drained depressions and in swamps, black spruce with tamarack or eastern white cedar, form well-marked communities."

Red Oak also occurs sporadically in drier upland areas, and Red Maple is common (often in association with Sugar Maple) in the understory of mesic sites .

DESCRIPTION OF FOREST-TYPES

Old-growth stands are those that have developed over a long period free of catastrophic disturbances (Franklin *et al.*, 1981). We define catastrophic as any disturbance that results in changing the dominant tree species in a stand.

In this study, old-growth and mature stands are both pine-dominated. Old-growth stands have no history of catastrophic disturbance for at least 150 years, and mature stands for approximately 100 years.

Managed stands were previously dominated by pine (aerial photographs, circa 1940). The pine was selectively logged roughly 50 years ago (i.e. the pine stand was catastrophically disturbed). The understory trees have now matured, so that these stands represent recently-disturbed forests in which the dominant trees are similar in age to mature or old-growth stands.

SITE SELECTION

Study sites were selected using information from the 1980 Forest Resource Inventory (FRI) data (Ontario Ministry of Natural Resources, based on 1977 aerial photography). This inventory of forested regions is carried out periodically to provide information on forest composition. Using aerial photographs, maps are produced which delineate forest stands: areas of forest dominated by similar vegetation. An estimate of the percent cover of the major tree species in the stand is provided, along with an estimate of average stand height, average stand age, stand area and site class (OMNR, 1992a; 1992b). Site class is a numerical expression of productivity, determined using Normal Yield Tables. There are five site classes: X, 1, 2, 3 and 4 with 'X' being the highest site quality and '4' the poorest site quality (OMNR, 1992b).

The FRI stand-age estimate was used as an indication of time since catastrophic disturbance for pine sites (i.e. the age of the dominant trees in the stand indicates that the pine stand has developed without catastrophic disturbance for at least that length of time). To verify FRI age estimates, tree-cores were used to age every pine encountered during the course of sampling in five mature and five old-growth stands (Appendix A.2). A regression equation was calculated between log(average core age) and log(FRI age).

Managed stands were selected with the advice of the Ontario Ministry of Natural Resources, Temagami District, based on knowledge of previous logging activities. Logging in the stands was verified by the presence of stumps, now rotted, and by evidence of old logging-roads, remnants of machinery and paint blazes on trees. Some large pines remain in managed stands along lake shorelines, as well as the occasional pine tree in the forest interior; these often bore a paint mark, probably indicating that they were not logged due to their size at the time or a "defect" (e.g. crooked trunk).

Twenty-nine sites were sampled: ten old-growth, nine mature, and ten managed (Appendix A.1). These twenty-nine sites correspond to twenty-two separate FRI forest stands.

Only one site was located in most stands; however, due to logistical constraints (e.g. travel time, availability of appropriate stands), seven stands contained two study sites each. These sites were separated by at least 500 m and were considered to be independent samples.

The intent in sampling as many separate forest stands as possible was to include a wide range of site conditions within old-growth, mature and managed forests. There was no strong bias in site class among forest types, although managed stands had slightly poorer site conditions in general (i.e. more class '3' stands) (Appendix A.2).

STUDY DESIGN

A 1-kilometer transect was laid out at each study-site, 100 m from any edge. Five 100 m cross-transects were located at 200-meter intervals along the main transect.

MEASUREMENT AND ANALYSIS OF VEGETATION DATA

Vegetation sampling was conducted in July and August, 1991 and 1992; measured characteristics are summarized in Table 2. Tree and snag density were measured using a modified point-distance nearest-neighbour technique (Batchelor, 1973) (Appendix B). Every 10 meters along both the main and cross-transects, the distance from the observer to the nearest stem (diameter>10 cm) was recorded, as well as tree species and diameter at breast height (dbh). This procedure was repeated to the first stem's "nearest neighbour", and to the second stem's "nearest neighbour". Total stem density, and density by species was calculated for each study site according to Batchelor (1973). Non-pine coniferous tree species were grouped, as were deciduous shade-tolerant (birch, aspen) and deciduous shade-intolerant (maple, ash, oak) tree species.

Since large trees are thought to be an important distinguishing characteristic of old-growth forests, tree densities were calculated for three size-classes: small (10-20 cm dbh), medium (21-50 cm dbh), and large (over 50 cm dbh). Mature Eastern White Pine (*Pinus strobus*) can attain diameters of 60-150 cm, and Red Pine (*Pinus resinosa*) between 60-90 cm (Grimm, 1983), depending on site conditions. The largest White Pine and Red Pine sampled in this study measured 94 cm dbh, and 70 cm dbh respectively. A regression was calculated for log(dbh) and log(average core age) of pines, to determine if age and diameter were related.

Vegetation cover in each of several strata (0 to 1 m, 1 to 8 m, 8 to 15 m and over 15 metres) was measured every 15 m along the transects. These strata were chosen to correspond to the following foliage profiles: ground-understory (0 to 1 m), low canopy (1 to 8 m), mid-canopy (8 to 15 m) and upper canopy (over 15 m). Measurements involved recording the species of trees and shrubs in each stratum which intercepted an imaginary line that started at the ground and extended upward through the canopy. Data were summed for each site and used to calculate percent cover per layer (the number of occurrences of foliage divided by the total number of points measured), the average number of tree and shrub species occurring in each layer, the average number of layers per stand with vegetation cover, and the variance in the number of layers (calculated among sampling points within a site). Percent cover and the average number of vegetation layers are indices of the vertical structure of the forest. The variability in the number of layers is an index of spatial diversity in vertical structure, while number of tree and shrub species is an index of vegetation diversity.

To determine if old-growth, mature and managed forests were structurally different, the variables describing vegetation structure were compared among forest-types using either one-way ANOVA, or if the assumptions of a parametric test could not be met, the Kruskal-Wallis test. As well, Spearman Rank Correlations were calculated between stand age and the vegetation variables.

A posteriori comparisons of ANOVA results were done using Tukey tests. For non-parametric tests, *a posteriori* comparisons were performed using multiple Mann-Whitney U-tests corrected for multiple comparisons.

Normality of residuals was evaluated using Lilliefor's test, and Bartlett's test was used to test for homoscedasticity (Appendix C). The following variables met the assumptions without transformation: densities of small trees, medium pine, large conifers, large shade-tolerant deciduous trees, and large snags. Density of large trees, small pine and large pine were transformed as $x' = \log(x + 0.5)$. All other density variables were transformed as $x' = (x + 0.5)^{1/2}$.

Power was calculated for non-significant parametric tests (Appendix D). Power is the probability of rejecting the null hypothesis when it is in fact false and should be rejected (Zar, 1984). Reported correlation coefficients values are adjusted:

$$r \text{ adjusted} = 1 - [n/\text{d.f.}\ (1-r)]$$

where n = sample number, d.f.= degrees of freedom.

Figure 1- Location of sampling sites in this study. Twenty-nine sites were sampled. Refer to Appendix A.1.

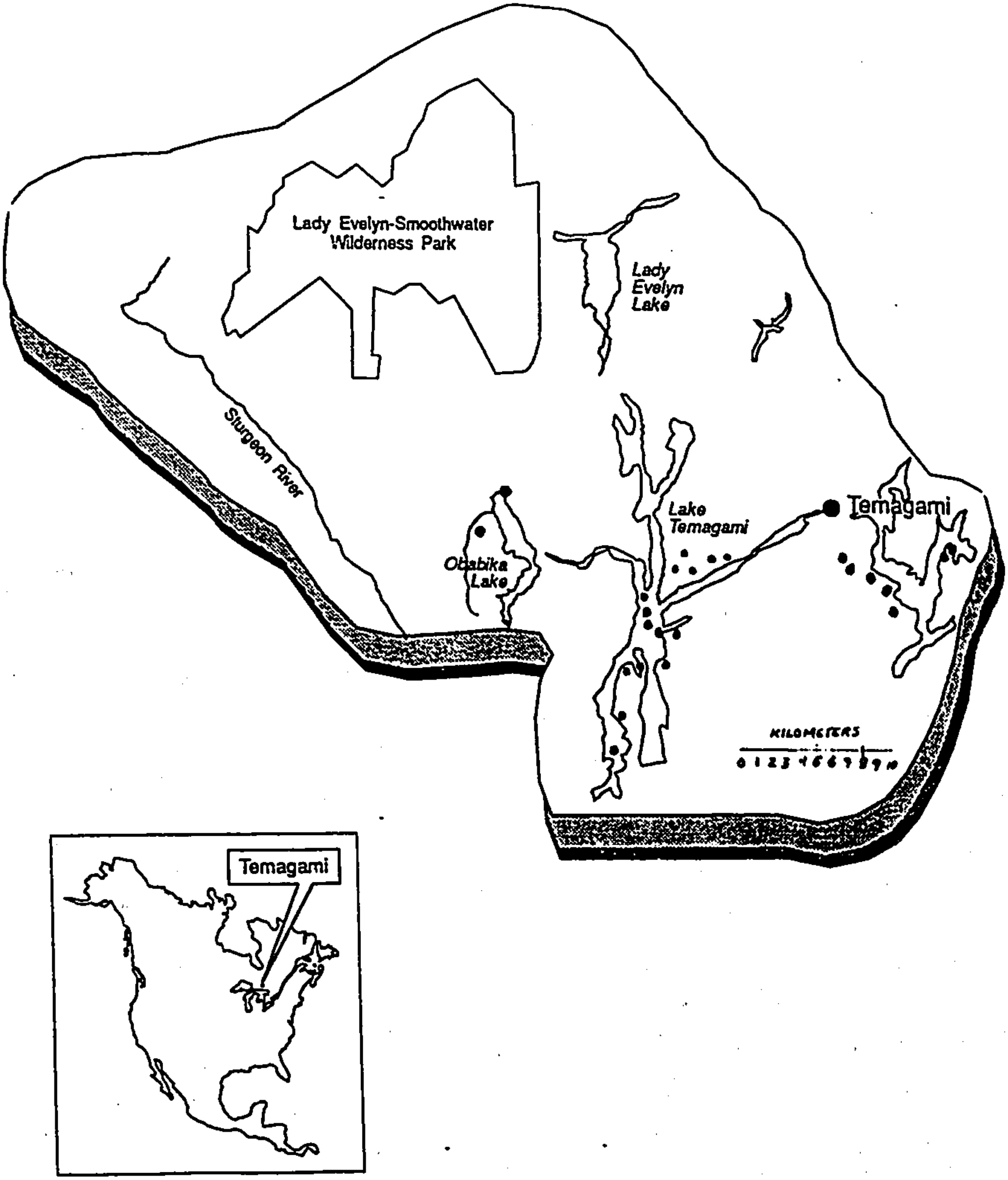

Lady Evelyn-Smoothwater
Wilderness Park
Lady
Evelyn
Lake
Sturgeon River
Obabika
Lake
Lake
Temagami
Temagami
KILOMETERS
0 1 2 3 4 5 6 7 8 9 10
Temagami

Table 2- Measures of vegetation structure and composition in old-growth, mature and managed forests.
(Density (stems/hectare); Height (meters)).

Variable
Total tree density
Density of trees in three size classes: 10-20 cm dbh (small) 20-50 cm dbh (medium) over 50 cm dbh (large)
Density of pine, non-pine conifer, deciduous shade-tolerant, deciduous shade-intolerant trees (also by size class)
Total snag density
Snag density in three size classes (10-20 cm, 20-50 cm, over 50 cm dbh)
Stand height
Average number of vegetation layers per stand
Variance in number of vegetation layers per stand
Number of tree and shrub species per layer (0-1 m, 1-8 m, 8-15 m, over 15 m)
Vegetation cover per layer (0-1 m, 1-8 m, 8-15 m, over 15 m)

RESULTS

Age

Stand-age estimates were well correlated with average core ages ($r^2=0.87$; $n=10$; $p<0.001$). However, a regression equation fitted to the data indicated that although this relationship held well for mature stands, it departed from a 1:1 relationship as stand-age increased (Fig. 2; Appendix A.3):

$$\log(\text{core age}) = 0.642 + 0.670 \log(\text{FRI age})$$

Although the FRI overestimated age for all old-growth sites, average core ages still placed mature and old-growth stands in two distinct groupings ($F_{1,8}=53.2$, $p=0.000$).

Tree Size

The three forest-types had similar distributions of tree-diameter measurements (Table 3, Fig. 3). Tree diameters ranged from 10-94 cm in old-growth, 9-84 cm in mature, and 10-98 cm in managed stands. Only a small proportion of trees in any stand were large. Trees greater than 50 cm were in the 95th percentile of tree diameter distribution in old-growth stands, and in the 97th percentile in mature and managed stands.

The overall densities of live stems did not differ significantly among forest-types, and neither did the densities of live stems in small, medium or large size classes (Table 3). However, the distribution of tree species in the three size classes did vary among forest-types (Table 3). Small deciduous shade-intolerant trees had higher densities in mature than managed stands, but neither differed significantly from old-growth stands. The density of medium-diameter pines was higher in old-growth and mature stands, while density of medium non-pine conifers was higher in managed stands. Medium-diameter non-pine conifers in managed stands were mostly Eastern White Cedar (*Thuja occidentalis*) (77.3%), followed by Black Spruce (*Picea mariana*) (12.6%), White Spruce (*Picea glauca*) (7.5%) and Balsam Fir (*Abies balsamea*) (2.6%).

The oldest stands do not necessarily contain the largest trees. The density of large pine was only weakly correlated with stand age (Table 5), and large pine density did not differ significantly between old-growth and mature stands (Table 3; Fig. 4). The correlation between average core age and tree diameter is significant, but quite weak ($r^2=0.21$; $n=282$; $p<0.000$) (Fig. 5):

$$\log(\text{coreage}) = 1.207 + 0.554 \log(\text{dbh})$$

The density of large non-pine conifers did not differ significantly among forest-types in *a posteriori* contrasts, although the initial comparison was significant (Table 3). All large non-pine conifers in managed sites were Eastern White Cedar, while in old-growth sites 57% were Balsam Fir and 43% Eastern White Cedar.

Snag Density

There were no significant differences among treatments in the overall density of snags (Table 3); however, their size distribution differed. The density of small snags was significantly higher in managed than in old-growth forests, while old-growth forests had significantly more large snags than did mature forests (Table 3).

Tree and Shrub Diversity

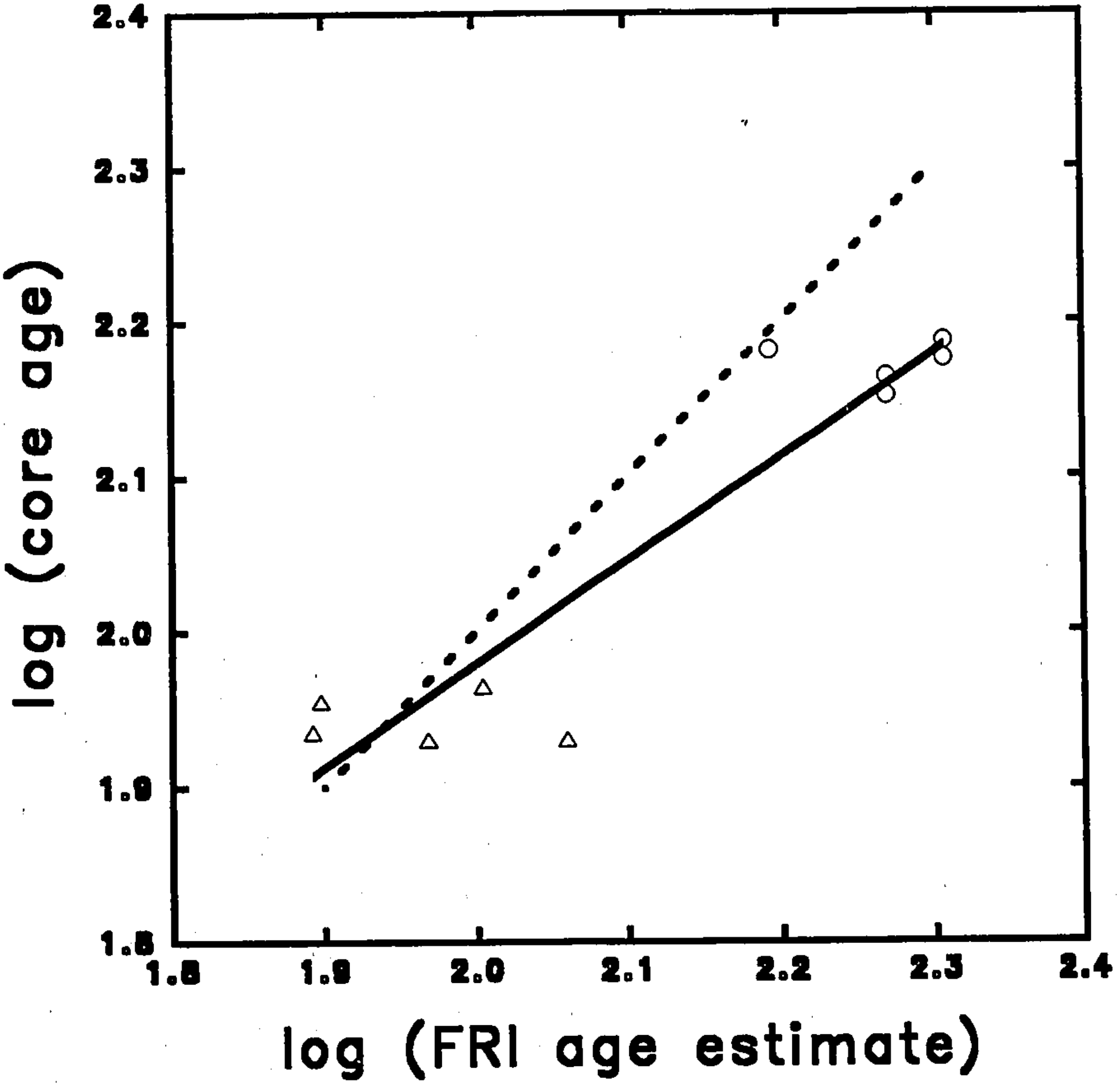
The vegetation of old-growth, mature and cut stands was very similar. Thirty-six species of trees and shrubs were encountered during vegetation sampling, twenty-six of which occurred in all three forest-types (Appendix E). Sugar Maple (*Acer saccharum*) and Mountain Holly (*Nemopanthus mucronata*) occurred only in old-growth stands, Juniper (*Juniperus virginiana*) and Red-twigged Serviceberry (*Amelanchier sanguinea*) occurred only in mature stands, while Raspberry (*Rubus idaeus*), and Red-Osier Dogwood (*Cornus stolonifera*) were only observed in managed stands. Red Oak (*Quercus rubra*) and Withe-Rod (*Viburnum cassinoides*) were never encountered in managed stands, neither was cherry (*Prunus* sp.) in old-growth stands, nor blueberry (*Vaccinium sp.*) in mature stands. The average number of species per layer did not differ significantly among treatments in the lower forest layers. However, old-growth had significantly more tree species on average in the 8 to 15 m and over 15 m layers (Table 4).

Structural Characteristics

Canopy-associated characteristics were the only structural features significantly related to stand age. The canopy of old-growth stands was significantly higher than in managed or mature stands, as was percent cover of vegetation in the upper canopy, average number of vegetation layers and variance in the number of layers (Table 4). Of all the vegetation variables measured, canopy height differed most strongly among forest-types ($r^2=0.560$)(Table 4), but was still highly variable within each group (Fig. 6).

Both measures of vertical diversity were strongly related to canopy structure. The average number of vegetation layers and variance in the number of layers were positively correlated with percent cover over 15 m, density of large and medium pine, and stand height (Table 5). Moreover, understory structure did not differ among forest-types. This indicates that the differences in vertical diversity observed among forest-types were due mainly to the presence of the upper canopy layer in old-growth stands. Variance in the number of layers was also weakly correlated with the density of small pine indicating a potential contribution of understory structure to the observed differences.

Figure 2- The relationship between log(average core age) (years) and log(FRI stand age estimate) (years) of red and white pine in five mature and five old-growth sites. The dashed line represents a 1:1 relationship; the solid line is the fitted regression equation. Circular symbols represent old-growth sites, and triangular symbols represent mature sites.



log (core age)
2.4
2.3
2.2
2.1
2.0
1.9
1.8
1.8
1.9
2.0
2.1
2.2
2.3
2.4
log (FRI age estimate)

Figure 3- The distribution of tree diameters in old-growth, mature and managed sites. The box represents the range between the 25th and 75th percentiles of the data; a horizontal line within the box marks the value of the 50th percentile. Capped bars indicate the 10th and 90th percentile points.

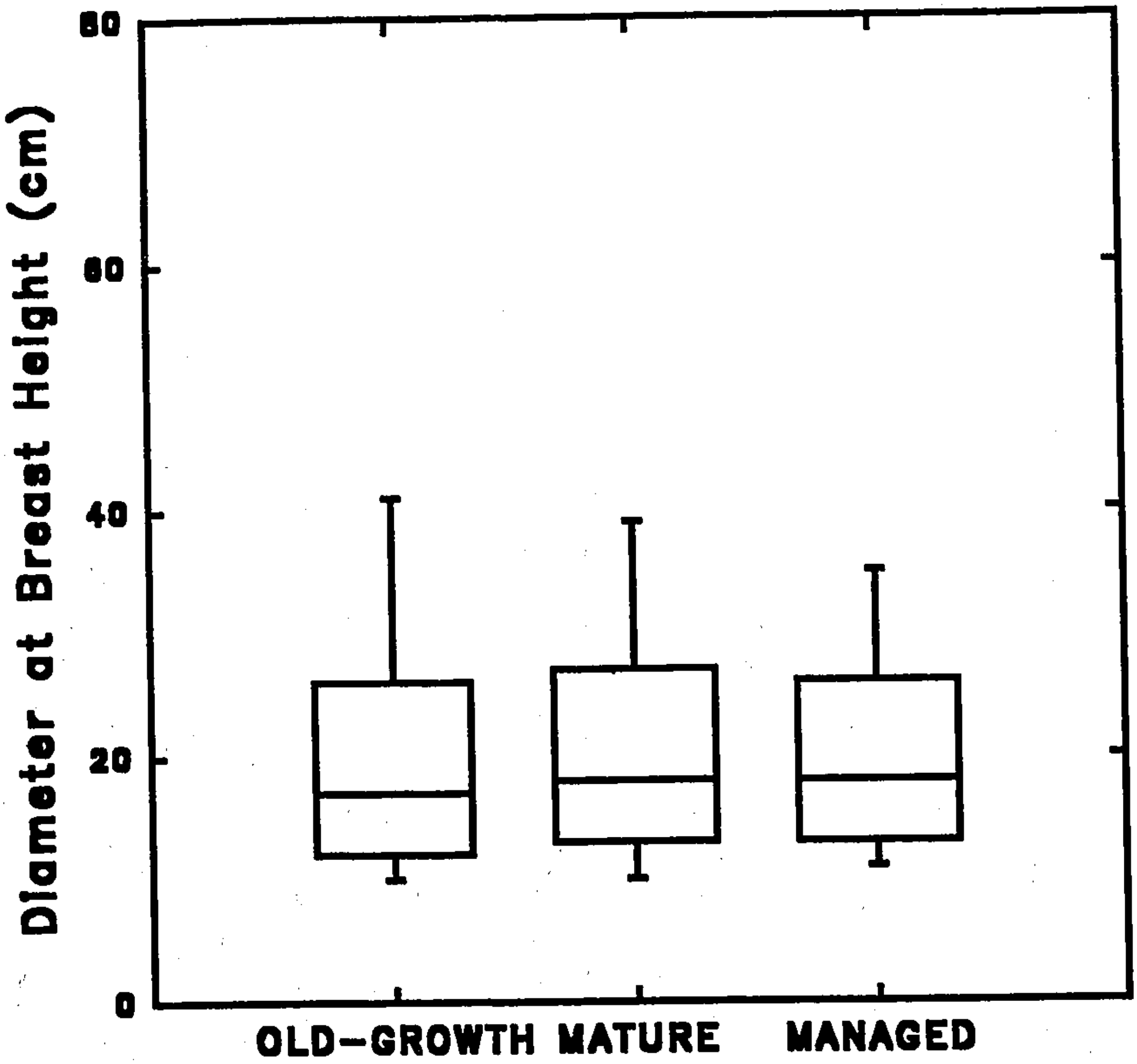
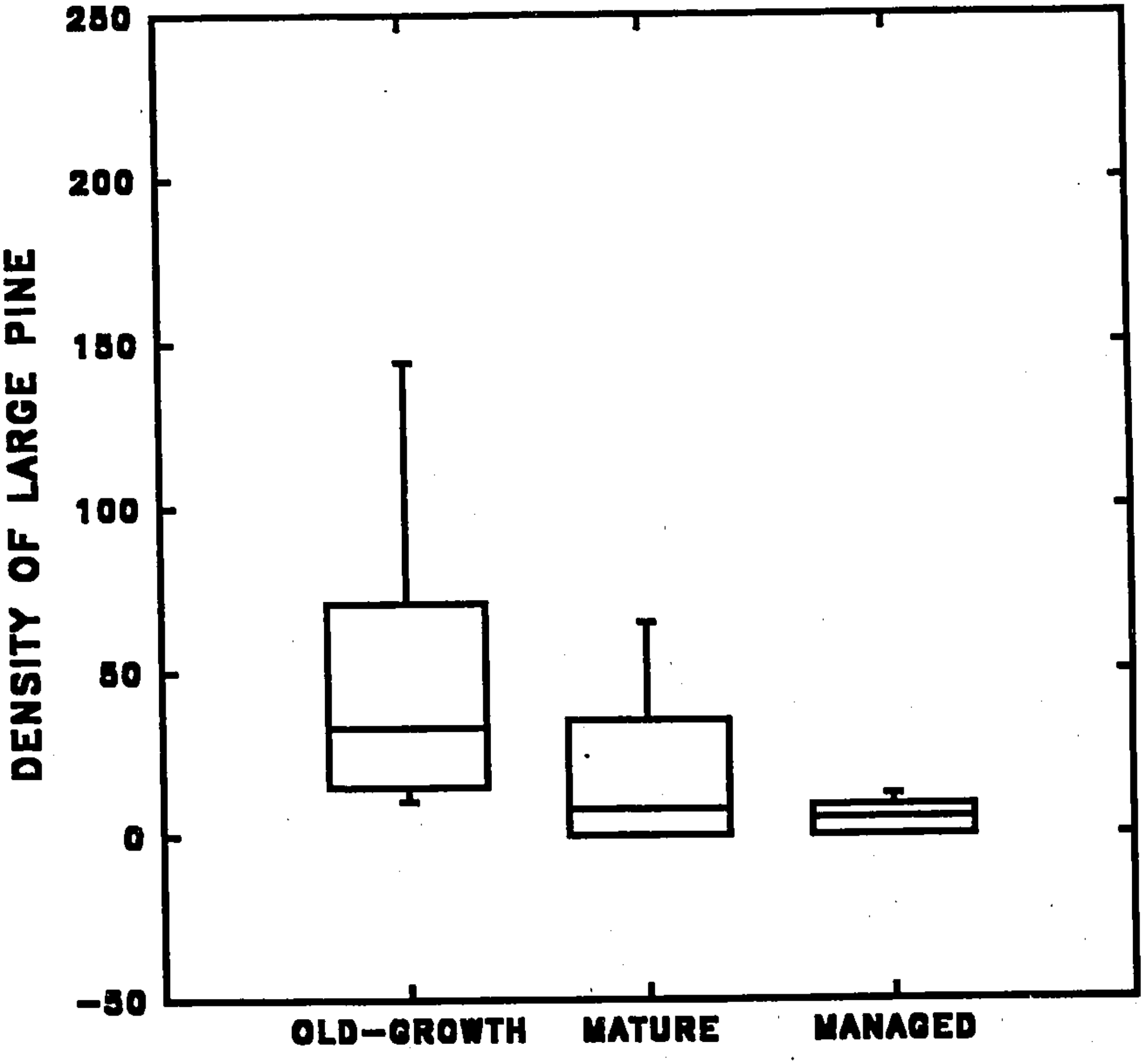

80
60
40
20
0
Diameter at Breast Height (cm)
OLD-GROWTH
MATURE
MANAGED

Table 3- Comparison of stem density of old-growth (og), mature (mt), and managed (mn) sites. Density is summed for all species and size-classes (all stems), and separated into size categories by diameter at breast height: small (10-20 cm), medium (21-50 cm), and large (over 50 cm). For each size class, density is reported for all species, pine, non-pine conifers (other conifer), deciduous shade-tolerant species (decid. s.t.), and deciduous shade-intolerant species (decid. s.i.). AOV = One-Way Analysis of Variance; K-W = Kruskal-Wallis. N=29. n.a.=not applicable. n.s. $p<0.05$

Dep Var	Test	F	P	r^2	*A posteriori* Contrast
TREE DENSITY					
all stems	AOV	0.38	n.s.	-	
SMALL STEMS					
all species	AOV	0.02	n.s.	-	
pine	AOV	2.71	n.s.	-	
other conifer	AOV	2.72	n.s.	-	
decid. s.t.	AOV	0.39	n.s.	-	
decid. s.i.	AOV	6.04	0.007	0.298	mt>mn;og=mn,mt
MEDIUM STEMS					
all species	AOV	0.72	n.s.	-	
pine	K-W	19.20	0.000	n.a.	og>mn;mt>mn;og=mt
other conifer	AOV	9.30	0.001	0.399	mn>og,mt;og=mt
decid. s.t.	AOV	0.56	n.s.	-	
decid. s.i.	K-W	0.88	n.s.	n.a.	
LARGE STEMS					
all species	AOV	2.92	n.s.	-	
pine	AOV	7.31	0.003	0.341	og>mn;og=mt;mn=mt
other conifer	K-W	4.01	0.030	n.a.	og=mt=mn
decid. s.t.	K-W	1.80	n.s.	-	
decid. s.i.	none				
SNAG DENSITY					
all sizes	AOV	2.51	n.s.	-	
small snags	AOV	5.73	0.009	0.286	mn>og;mt=og,mn
medium snags	AOV	0.48	n.s.	-	
large snags	K-W	4.48	0.020	n.a.	og>mt;mn=mt,og

Figure 4- The density of pine trees > 50 cm in diameter at breast height in old-growth, mature and managed sites. The box represents the range between the 25th and 75th percentiles of the data; a horizontal line within the box marks the value of the 50th percentile. Capped bars indicate the 10th and 90th percentile points.



DENSITY OF LARGE PINE
250
200
150
100
50
0
−50
OLD−GROWTH
MATURE
MANAGED

Figure 5- The relationship between log(average core age) (years) and log(diameter at breast height)(meters) for red and white pine. N=282. Note that although the relationship would be weaker if outliers were excluded, their inclusion still results in a weak correlation and does not change our conclusions.

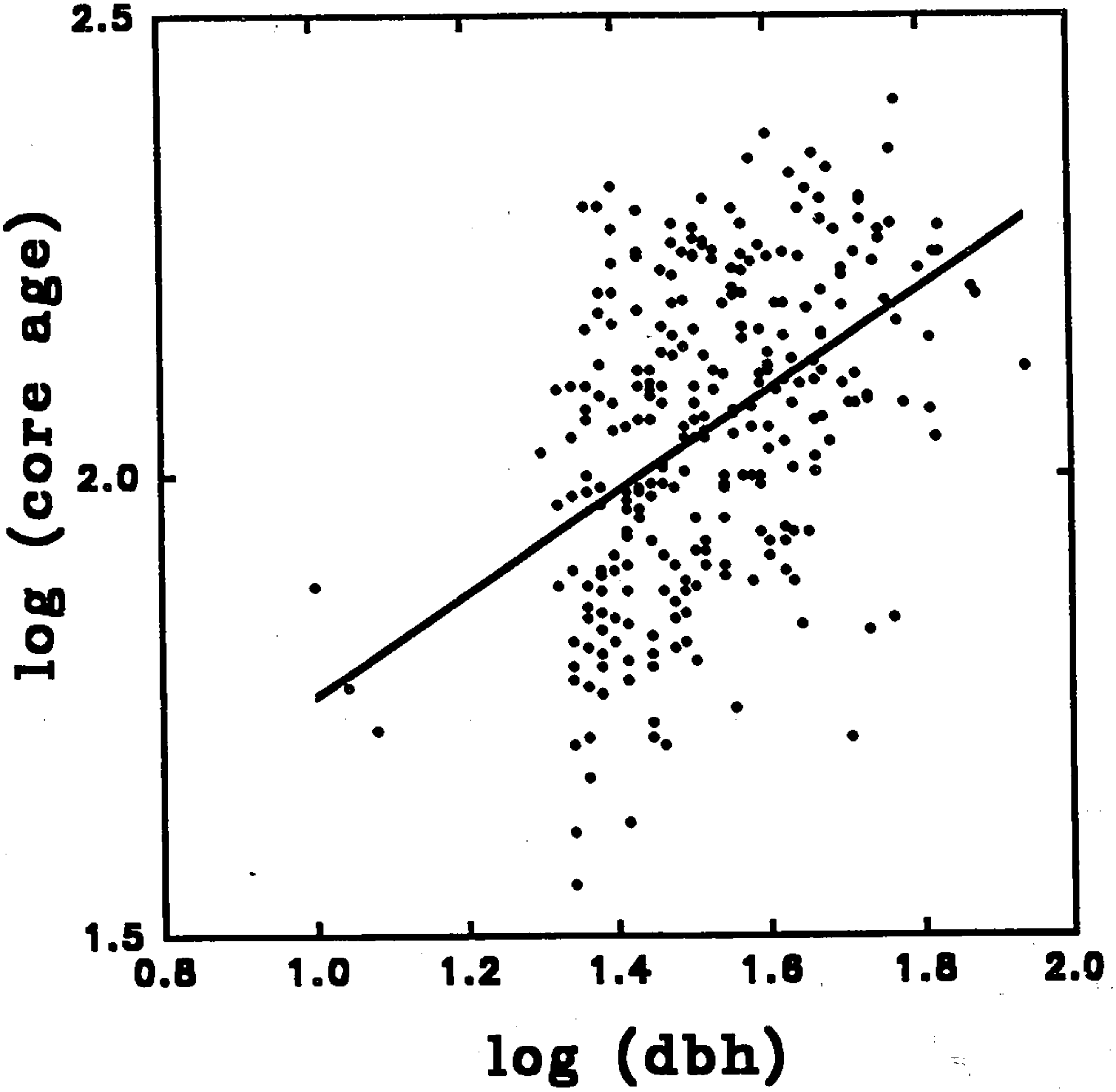

2.5
2.0
1.5
0.8
1.0
1.2
1.4
1.6
1.8
2.0
log (core age)
log (dbh)

Table 4: Comparison of vegetation characteristics of old-growth, mature and managed stands: stand height (meters), average number of layers (LAYERS), variance in the number of layers (VARLAY), number of species per layer and percent cover per layer. Number of species and percent cover are subdivided into four strata: 0 to 1 meters, 1 to 8 meters, 8 to 15 meters and over 15 meters. AOV=ANOVA; K-W=Kruskal-Wallis. N=29.
n.a. = not applicable

Dep var	Test	F	P	r^2	*A posteriori* contrast
STAND HEIGHT	AOV	17.50	0.000	0.560	og>mt,mn;mt=mn
LAYERS	AOV	10.70	0.000	0.434	og>mt,mn;mt=mn
VARLAY	AOV	7.62	0.003	0.349	og>mt,mn;mt=mn
NUMBER OF SPECIES					
0-1	K-W	0.46	n.s.	-	
1-8	AOV	0.54	n.s.	-	
8-15	AOV	4.55	0.020	0.239	og>mt,mn;mt=mn
over 15	K-W	9.47	0.003	n.a.	og>mt,mn;mt=mn
PERCENT COVER					
0-1	AOV	2.42	n.s.	-	
1-8	K-W	2.52	n.s.	-	
8-15	AOV	4.10	0.028	0.220	og>mn;mt=og,mn
over 15	K-W	13.72	0.000	n.a.	og>mt,mn;mt=mn

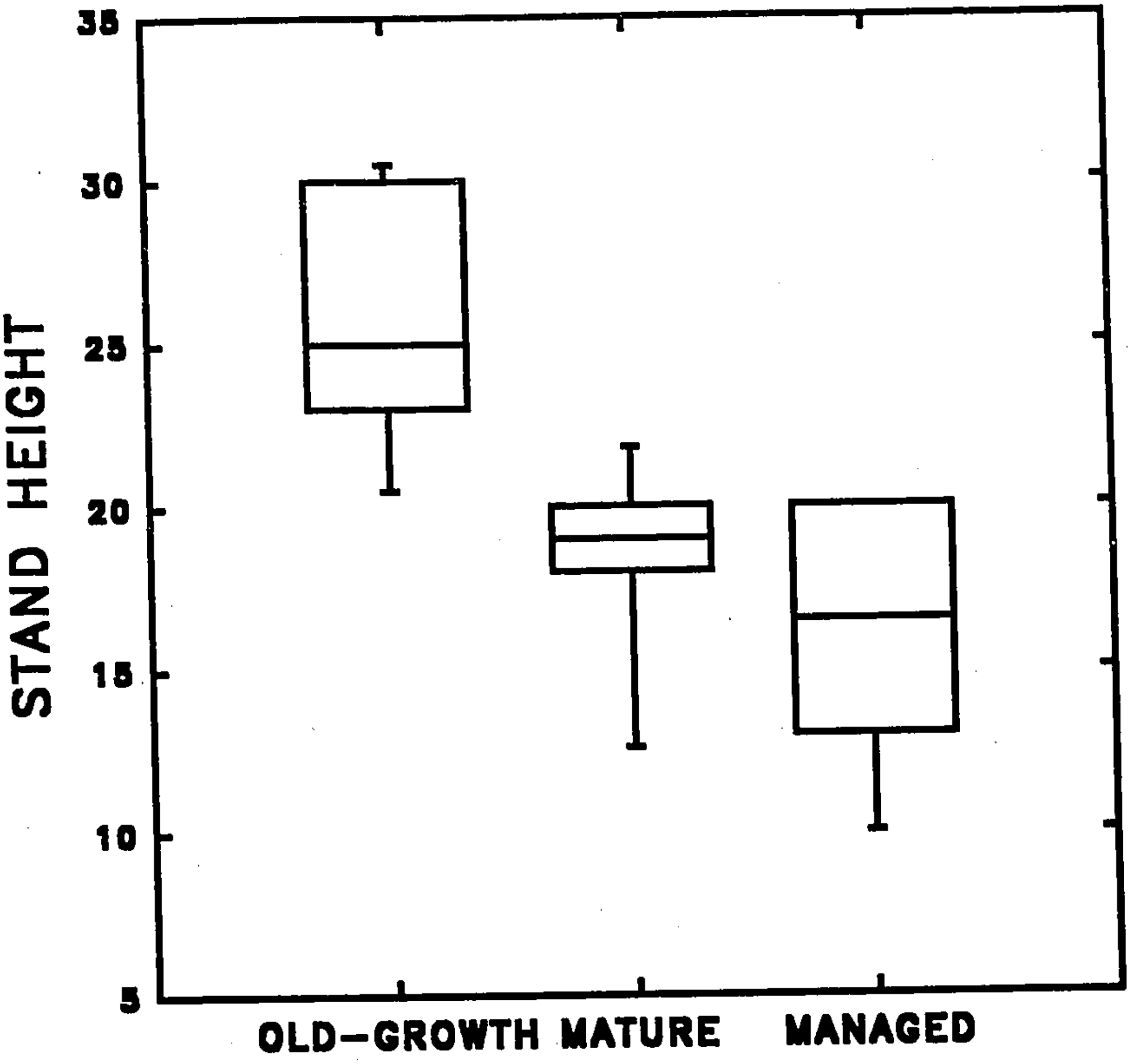
n.s. p>0.05

Table 5- Spearman Rank Correlations among FRI Stand Age (years), average number of layers (LAYERS), and variance in the average number of layers (VARLAY) with stand height (meters), number of species over 15 m (SPOV15), number of species in the 8 to 15 m layer (SP8TO15), percent cover over 15 m (COVOV15), density of small pine (DENPINS), density of medium pine (DENPINM) and density of large pine (DENPINL). N=29.

	AGE	LAYERS	VARLAY
AGE	-	0.395*	0.393*
LAYERS	0.395*	-	0.522**
VARLAY	0.393*	0.456*	-
HEIGHT	0.558**	0.456*	0.427*
SPOV15	0.619**	n.s.	n.s.
SP8TO15	0.405*	n.s.	0.447*
COVOV15	0.561**	0.677***	0.556**
DENPINS	n.s.	n.s.	0.370*
DENPINM	n.s.	0.403*	0.432*
DENPINL	0.438*	0.619**	0.417*

n.s. $p>0.05$
* $p<0.05$
** $p<0.005$
*** $p<0.001$

Figure 6- Estimated stand height (meters) from Forest Resource Inventory in old-growth, mature and managed sites. The box represents the range between the 25th and 75th percentiles of the data; a horizontal line within the box marks the value of the 50th percentile. A capped bar indicates the 10th and 90th percentile points. For managed stands, the 90th percentile equates the 75th percentile.



STAND HEIGHT
35
30
25
20
15
10
5
OLD-GROWTH
MATURE
MANAGED

DISCUSSION

Clearly, not all types of old-growth forests have the same structural attributes. The density of large-diameter trees was found to distinguish old-growth and mature Douglas-fir stands (Bingham and Sawyer, 1991; Carey *et al.*, 1991; Huff *et al.*, 1991; Spies and Franklin, 1991). In contrast, large tree density did not differ among eastern old-growth pine forests, mature and managed forests. On the other hand, our result is consistent with studies of forests of the central hardwood region of the United States (Muller, 1982), and an eastern deciduous forest of Quebec (Brisson and Bergeron, 1992). Large snag density was also found to be a distinguishing characteristic of old-growth Douglas-fir stands (Carey *et al.*, 1991; Huff *et al.*, 1991). Large snag density was higher in old-growth than in mature pine stands, but did not differ between old-growth and managed, nor mature and managed stands. The difference observed between old-growth and mature pine stands is likely due to age (greater tree death in old stands). The intermediate density of snags in managed stands may be due to past management practices (i.e. if snags were left standing after cutting).

The observed discrepancies between eastern and western forests may be due to differences in variability within forest-types as a consequence of local edaphic factors. Spies and Franklin (1991) sampled only mesic sites in their comparison of age-classes, while Huff *et al.* (1991) do not provide this information. Bingham and Sawyer (1991) and Carey *et al.* (1991) sampled a gradient of site moisture classes. Bingham and Sawyer (1991) report that the standard errors of large tree and large snag densities were less than 20% of the age-class mean. Our results show standard errors between 33-36% of mean large tree density, and between 55-70% of mean large snag density (Appendix F). This greater variability may be due to a different range of site conditions measured, or perhaps development of eastern pine forests is more sensitive to local site variability than in western forests.

Old-growth pine forests did not have greater vegetation (i.e. tree and shrub) species diversity. There were two vegetation species which occurred uniquely in each of the three forest-types. Raspberry and Red-Osier Dogwood, which are often associated with disturbed sites and increased canopy opening, were found only in managed stands. Cherry, another disturbance-related species was never encountered in old-growth stands. The other "unique" species (Sugar Maple and Mountain Holly in old-growth sites and Juniper and Red-twigged Serviceberry in mature stands) are commonly found elsewhere and their occurrence was likely attributable to local site conditions.

Most old-growth pine stands, like old-growth Douglas-fir stands, have high canopies. Stand height, number of species and percent cover in the upper canopy, number of vegetation layers and spatial variability in the number of layers were all significantly higher in old-growth pine forests than in more recently disturbed stands. All of these statistics reflect the greater prevalence of tall trees in old-growth pine stands.

However, although statistically significant, differences in canopy-related characteristics among old-growth, mature and managed forests were not strong due to the high variability among individual stands (within each forest-type). This variability is due to the influence of site conditions and developmental history in determining the structural characteristics of each forest stand. The frequency of non-catastrophic fires, wind throws, and intensity of cutting in the case of managed forests, vary among stands. Low-intensity fires may result in decreased density of small stems, while leaving large trees standing, and may also increase snag density. Wind throws reduce stem density and increase the amount of fallen dead wood. Site conditions (e.g. moisture, soil depth) also influence stand structure. For example, the size that trees attain depends on growing conditions, which probably explains the low correlation between core age and stem diameter of pines. Site moisture is also related to fire occurrence and intensity, and decay rates (Spies *et al.*, 1988).

One problem in comparing groups of forest stands is the possibility that structural differences observed are due to a bias in site conditions, rather than age and disturbance history. For instance, that the managed sites are, as a group, somehow different and were cut for that reason (e.g. that they were in low, easily-accessible terrain). However, the site quality measurements were comparable among groupings. Site conditions were slightly poorer in managed sites, yet tree diameters did not differ significantly from mature and managed sites, indicating that this bias was not strong. A more thorough description of topography, soil and aspect would provide more information in this regard.

This effect of site conditions must not be ignored in attempting to characterize old-growth forest ecosystems. Franklin *et al.* (1981) state that development of old-growth conditions is faster on good sites than on poor sites. Similarily, the Old-Growth Definition Task Group (1986) has proposed that a Douglas-fir stand will be considered to be old-growth if it meets minimum standards of snag, log and old-tree density. This circular line of reasoning defines old-growth by a set of chosen criteria rather than concluding that all "old, undisturbed forests" have a particular set of ecological characteristics.

Management and Conservation Implications

Preservation of the measured habitat characteristics will entail conservation of late-successional stands, and/or allowing forests to develop on a long-rotational basis. All these characteristics develop as forests age. Age appears to be more important than disturbance in the development of these particular habitat characteristics. The managed stands sampled were undisturbed only fifty years after selective cutting. The average age of the dominant trees in the three forest-types ranged between 88-186 years (Appendix A.1). The length of rotation necessary for development of these characteristics has yet to be determined. The requirements of species for these habitat characteristics in eastern forests is also unknown.

Eastern old-growth pine forests were not found to provide unique habitat as related to snag density, large tree density or canopy structure. There was a great deal of overlap in these characteristics among old-growth, mature and managed stands. Therefore, insofar as a goal of forest management is preservation of these habitat characteristics than forest-type is a poor criterion for their preservation. Rather, conservation should be based at the level of individual stand characteristics.

Old-growth pine forests may provide unique habitat if both structure and vegetation are important to a species occurrence. Past intensive cutting of pine in Temagami resulted in changing the dominant tree species in managed stands. Therefore, although structurally similar, they do not necessarily present similar habitat (i.e. for pine ecosystem specialist species). Managed stands were similar to old-growth in all characteristics, except large snag density. Species requiring large snags, and pine habitat may occur more frequently in old-growth forests. It is unknown how low-level selective cutting will affect these habitat parameters in old-growth stands.

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APPENDIX A.1- Forest stand descriptions from a 1980 forest resource inventory based on 1977 aerial photographs. Site No.=sampling site designation (MN=managed stands, OG=old-growth stands, MT=mature stands); Site Class[1]; FRI No.=stand designation for forest resource inventory[2]; Species Composition=proportion[3] of tree species[4] estimated from aerial photographs; Age (years)=estimate of age of dominant tree species from aerial photographs; Height (meters)=estimate of stand height from aerial photographs; Area (hectares).

Site No.	Site Class	FRI No.	Species Composition	Age	Ht.	Area
MN0	3	St38	Sb3Sw2B2Pw1Bw1Ce1	91	10	165
MN1	2	B46	Bw4Po3Sw2Ab1	111	20	81
MN2	3	B38	Sw2Sb1Pw2Ce2Bw1Mh1By1	173	19	210
MN3	2	D66	Sb6Sw2Bw1B1	101	14	155
MN4	2	J29	Bw5Po2Sw1Pr1Pw1	96	20	137
		J30	Bw4Po3Pj2Sb1	91	20	129
MN5	2	B46	Bw4Po3Sw2Ab1	111	19	81
MN6	3	B38	Sw2Sb1Pw2Ce2Bw1Mh1By1	173	14	210
MN7	2	J29	Bw5Po2Sw1Pr1Pw1	96	20	137
		J30	Bw4Po3Pj2Sb1	91	20	129
MN8	3	St80	Sb2Sw2Ce3Ab2Bw1	122	13	138
MN9	3	St38	Sb3Sw2B2Pw1Bw1Ce1	91	10	165
			AV. AGE	135		
OG0	2	P72	Pw4Po1Bw1Ce1Pr1Sb1B1	196	30	66
OG1	3	P52	Pw4Mh2By2Ce1Bw1	226	22	185
OG2	2	P56	Pw6Mh2Pr1Ms1	203	30	255
		J84	Pw6Mh2Pr1Ms1	203	30	87
OG3	3	P65	Pr4Pw3Bw2Po1	156	19	127
OG4	1	V45	Pw6Bw1Po1Ms1B1	179	31	139
OG5	2	P44	Pr5Pw3Bw1Po1	153	23	140
OG6	2	S123	Pw4Pr2Sb1Bw1Ce1B1	186	25	808
		D34	Pw4Pr2Sb1Bw1Ce1B1	186	25	489
OG7	2	P56	Pw6Mh2Pr1Ms1	203	30	255
		J84	Pw6Mh2Pr1Ms1	203	30	87
OG8	2	R97	Pr5Pw2Bw1Po1Sw1	183	24	111
OG9	2	S123	Pw4Pr2Sb1Bw1Ce1B1	186	25	808
		D34	Pw4Pr2Sb1Bw1Ce1B1	186	25	489
			AV. AGE	275		
MT1	2	P38	Pw3Pr3Pj1Sb1Po1Bw1	93	20	70
MT2	1	P74	Pw4Po2Pr2Sw1Bw1	79	23	36
MT3	2	E127	Pw4Pj2Pr1Sw1Po1Bw1	88	19	74
MT4	2	R162	Pw4Pr2Bw2Po1Sb1	83	19	59
MT5	2	V113	Pr4Pw3Po1Bw1Sw1	115	20	253
		V35	Pr4Pw3Po1Bw1Sw1	115	20	171
MT6	2	J52	Pw3Pr3Sb6Bw2Po1	78	19	52
MT7	4	R165	Pw7Bw2Po1	93	11	66
MT8	3	P66	Bw3Pw2Pr2Po2Ce1	101	15	206
MT9	2	E127	Pw4Pj2Pr1Sw1Po1Bw1	88	19	74
			AV. AGE	104		

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[3] e.g.Pw7Bw2Po1= 70% White Pine, 20% White Birch, 10% Poplar

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APPENDIX A.1 - cont'd

[1] Site Class: A numerical expression of productivity of an area for a given species, determined from the appropriate figure in the normal yield table and expressed to the nearest full number. There are four site classes: X, 1, 2, 3 and 4 with X representing best site conditions, and '4' the poorest (Taken from Forest Resource Inventory maps).

Township Codes[2]
B- Briggs
D- Delhi
E- Eldrige
J- Joan
P- Phyllis
R- Riddell
S- Shelburne
St- Strathcona
V- Vogt

Species Codes[4]
Ab- Black Ash
B- Balsam Fir
Bw- White Birch
By- Yellow Birch
Ce- Cedar
Mh- Sugar Maple
Ms- Red Maple
Pj- Jack Pine
Po- Poplar
Pr- Red Pine
Pw- White Pine
Sb- Black Spruce
Sw- White Spruce

APPENDIX A.2- Number of study sites in each of 5 site classes (X, 1, 2, 3, 4). Site classes are determined from Forest Resource Inventory data, where 'X' is highest site quality and '4' is poorest.

		Old-growth	Mature	Managed
Site Class:	X	0	0	0
	1	1	1	0
	2	7	6	5
	3	2	1	5
	4	0	1	0
TOTAL		10	9	10

APPENDIX A.3- Age of the dominant tree species in selected stands obtained from Forest Resource Inventory surveys (FRI Age)(years) compared to average ages ± S.E. (n) determined by core sampling (Core Age) (years).

Forest Type	Stand No.	FRI Age	Core Age
Old-growth	P56/J84	203	154±6 (17)
Old-growth	P65	156	152±9 (30)
Old-growth	Sh123/D34	186	146±6 (20)
Old-growth	P56/J84	203	150±11 (16)
Old-growth	Sh123/D34	186	142±3 (39)
Mature	P38	93	85±18 (7)
Mature	P74	79	90±3 (16)
Mature	V113/V35	115	85±5 (18)
Mature	J52	78	86±5 (28)
Mature	P66	101	92±4 (31)

APPENDIX B- Method of calculation of the point-distance nearest-neighbour distance estimate of density (from Batcheler, 1973).

Defining the nearest neighbour to the sampling point as Ip, its nearest neighbour as In, and In's nearest neighbour as Im, the distances measured to these points are rp, rn and rm, and the number of these points sampled are p, n and m respectively . Distances were measured up to a chosen maximum distance R (in this study, 10 metres). The number of sample points, N, equals p, n, and m in this case where the maximum distance was never surpassed.

These data are used to calculate:

$$f = p/N$$

$$d = p/[\pi(\Sigma rp^2 + N - pR^2)]$$

$$A_1 = 1/E(CV)\sqrt{[p\Sigma rp^2 - (\Sigma rp)^2]n^2N/\Sigma rp\Sigma rnp^3....}$$

$$A^2 = 1/E(CV)\sqrt{[p\Sigma rp^2 - (\Sigma rp)^2]m^2N/\Sigma rp\Sigma rmp^2n}$$

in which A_1 and A_2 are two indices of non-randomness, and E(CV) is the expected coefficient of variation of rp (Batcheler, 1973, Table 2),

$$a = (1 + 2.473f)$$

$$b = (1 + 2.717f)$$

and $D = d/2a(b^{A1} + b^{A2})$

where D is the estimate of density.

APPENDIX C- Results of normality and homoscedasticity tests for One-Way ANOVA's described in Tables 2 and 3.

Dep Var	Normality	Homoscedasticity
Stand Height	p>0.164	p>0.839
Density of all trees	p>0.200	p>0.671
Density small pine trees	p>0.652	p>0.989
Density small non-pine conifer trees	p>0.728	p>0.311
Density small deciduous shade-tolerant trees	p>0.576	p>0.845
Density small deciduous shade-intolerant trees	p>0.057	p>0.150
Density all medium trees	p>0.209	p>0.598
Density medium non-pine conifer trees	p>1.000	p>0.077
Density medium deciduous shade-tolerant trees	p>0.200	p>0.681
Density all large trees	p>0.245	p>0.101
Density all large pine	p>0.129	p>0.112
Density of all snags	p>0.124	p>0.132
Density small snags	p>0.059	p>0.641
Denstiy medium snags	p>0.139	p>0.226
Average number of layers	p>0.556	p>0.601
Variance in no. of layers	p>0.060	p>0.362
No. of species in 1-8 m layer	p>0.844	p>0.742
No. of species in 9-15 m layer	p>0.844	p>0.093
Percent cover in 0-1 m layer	p>1.000	p>0.509
Percent cover in 9-15 m layer	p>0.673	p>0.839

APPENDIX D- Results for Power analysis of One-Way ANOVA results described in Tables 2 and 3.

Dep Var	P	Power
density of all trees	0.688	0.049
density of all small trees	0.930	0.049
density of small pine	0.082	0.164
density of small non-pine conifer	0.084	0.332
density small deciduous shade-tolerant trees	0.680	0.049
density of all medium trees	0.497	0.049
density medium deciduous shade-tolerant trees	0.575	0.049
density of all large species	0.072	0.356
density of all snags	0.101	0.327
density of medium snags	0.622	0.490
number of species in 1-8 m layer	0.591	0.048
percent cover in 0-1 m layer	0.109	0.267

Appendix E- Presence of tree and shrub species (indicated by '+') sampled using the point-cover method in layers: 0 to 1 m (1), 1 to 8 m (2), 8 to 15 m (3) and over 15 m (4).

SPECIES[1]	OLD-GROWTH				MATURE				MANAGED			
	1	2	3	4	1	2	3	4	1	2	3	4
Alder	+	+			+	+			+	+		
Black Ash		+	+			+				+	+	
Balsam Fir	+	+	+		+	+			+	+	+	
Beaked Hazel	+	+			+	+			+	+		
Blueberry	+								+			
Birch, White	+	+	+	+	+	+	+	+		+	+	+
Birch, Yellow	+	+	+	+		+	+			+	+	
Eastern White Cedar	+	+	+	+	+	+			+	+	+	+
Cherry					+	+			+	+		
Red-Osier Dogwood	+											
Fern	+				+				+	+		
Fly Honeysuckle	+				+				+			
Juniper					+	+						
Labrador Tea	+				+				+			
Larch		+	+	+	+	+			+			
Laurel	+								+			
Large-leafed Aster	+				+				+			
Large-toothed Aspen		+	+	+		+	+	+		+	+	+
Mountain Ash	+	+			+	+			+	+		
Mountain Holly	+	+										
Mountain Maple	+	+	+		+	+	+	+	+			
Northern Bush Honeysuckle	+	+							+	+		
Oak, Red		+	+	+	+	+	+	+				
Pine, Jack				+								
Pine, Red	+	+	+	+		+	+	+	+	+	+	+
Pine, White	+	+	+	+	+	+	+	+	+	+	+	+
Raspberry									+			
Red Maple	+	+	+	+	+	+	+		+	+	+	+
Red-twigged Serviceberry					+	+						
Sasparilla	+				+				+			
Sugar Maple	+			+						+		
Spruce, Black	+		+	+	+	+	+		+	+	+	+
Spruce, White	+		+		+	+	+		+	+	+	+
Striped Maple	+		+		+	+			+	+		
Trembling Aspen			+	+		+	+	+		+	+	+
Withe-Rod		+	+		+							
Willow					+	+				+		

[1]- Latin names are appended

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Appendix E- cont'd

^{1}- Scientific Names of Vegetation Species

Alder	*Alnus sp.*
Black Ash	*Fraxinus nigra*
Balsam Fir	*Abies balsamea*
Beaked Hazel	*Corylus cornuta*
Blueberry	*Vaccinium sp.*
Birch, White	*Betula papyrifera*
Birch, Yellow	*Betula alleghaniensis*
Eastern White Cedar	*Thuja occidentalis*
Cherry	*Prunus sp.*
Red-Osier Dogwood	*Cornus stolonifera*
Fern	*spp.*
Fly Honeysuckle	*Lonicera canadensis*
Juniper	*Juniperus virginiana*
Labrador Tea	*Ledum groenlandicum*
Larch	*Larix laricina*
Laurel	*Kalmia sp.*
Large-leafed Aster	*Aster macrophyllus*
Large-toothed Aspen	*Populus grandidentata*
Mountain Ash	*Sorbus decora*
Mountain Holly	*Nemopanthus mucronata*
Mountain Maple	*Acer spicatum*
Northern Bush Honeysuckle	*Diervilla lonicera*
Oak, Red	*Quercus rubra*
Pine, Jack	*Pinus banksiana*
Pine, Red	*Pinus resinosa*
Pine, White	*Pinus strobus*
Raspberry	*Rubus idaeus*
Red Maple	*Acer rubrum*
Red-twigged Serviceberry	*Amelancier sanguinea*
Sarsaparilla	*Aralia nudicaulis*
Sugar Maple	*Acer saccharum*
Spruce, Black	*Picea mariana*
Spruce, White	*Picea glauca*
Striped Maple	*Acer pennsylvanicum*
Trembling Aspen	*Populus tremuloides*
Withe-Rod	*Viburnum cassinoides*
Willow	*Salix sp.*

APPENDIX F- Mean, standard error (S.E.) and standard error as a percent of the mean of large tree density and large snag density in old-growth mature and managed stands.

Forest-Type	Mean Large Tree Density ± Standard Error (S.E. as % of mean)	Mean Large Snag Density ± Standard Error (S.E. as % of mean)
Old-Growth	17.8 ± 6.6 (36.0%)	17.8 ± 12.5 (70.2%)
Mature	24.3 ± 9.7 (36.0%)	0 ± 0
Managed	60.0 ± 19.8 (33.0%)	5.8 ± 3.2 (55.1%)

CHAPTER 2

Bird Abundance and Habitat Associations in Second- and Old-Growth Forests of the Temagami region of northern Ontario.

ABSTRACT

Old-growth Douglas-fir (*Pseudotsuga menziesii*) forests of the Pacific North-west are believed to provide important wildlife habitat not found in other forests. In this study we compare the abundance of eight bird species in three forest types in the Temagami region of northern Ontario: old-growth pine forests (no history of catastrophic disturbance for at least 150 years), mature pine forests (undisturbed for approximately 100 years) and managed forests (previously pine-dominated and selectively-cut roughly 50 years age).

Pine Warbler (*Dendroica pinus*) abundance was higher in old-growth and mature, compared to managed forests, while Solitary Vireo (*Vireo solitarius*), Blackburnian Warbler (*Dendroica fusca*) and Black-throated Green Warbler (*Dendroica virens*) tended toward higher abundance in old-growth than in managed stands ($0.05<p<0.10$), with abundance in mature forests intermediate between the two.

Pine Warbler abundance was strongly related to vegetation characteristics (canopy height, density of medium-sized pine and number of tree species in the upper canopy; $r^2=0.70$; $F_{3,25}=22.63$). Relationship between other species abundances and habitat variables were significant but not strong ($0.38<r<0.52$). Forest type did not explain a significant amount of the residual variance in abundances once that accounted for by vegetation characteristics was

removed.

INTRODUCTION

Logging is thought to influence the distribution of breeding birds by modifying their habitat (Haapenen, 1965; Webb *et al.*, 1977; Crawford *et al.*, 1981). Since bird communities are strongly related to the structure and composition of vegetation (Nilsson, 1979; Rice *et al.*, 1984; Rotenberry, 1985; Thompson and Capen, 1988) it is not surprising that different bird communities are associated with different forest-types (Welsh, 1985; Thompson and Capen, 1988). Significant alterations to the distribution of forest-types in the landscape as a result of logging may therefore impact avian populations. Of particular concern is the reduction in the amount of old-growth forest; these forests are not being replaced due to management for younger, faster-growing forests, managed on short-rotational cutting schedules.

Some bird species are more abundant in old-growth than in younger Douglas-fir forests of the north-western United States (Huff and Raley, 1991; Huff *et al.*, 1991; Lundquist and Mariani, 1991; Manuwal, 1991; Ralph *et al.*, 1991) but none of these species are unique to old-growth forests. However, to the extent that abundance reflects breeding success, reduction of old-growth habitat may result in population declines for these species, particularly those which make extensive use of old-growth Douglas-fir habitat (e.g. Vaux's Swift (*Chaetura vauxi*) (Lundquist and Mariani, 1991), Spotted Owl (*Strix occidentalis caurina*) (Forsman *et al.*, 1984), and Marbled Murrelet (*Brachyramphus marmoratus*) (Leschner and Cummins, 1992; Paton *et al.*, 1992)).

The greater abundance of some species in old-growth Douglas-fir forests compared to younger forests has been attributed to differences in habitat structure (Franklin *et al.*, 1981). Old-growth Douglas-fir forests have higher densities of large trees and snags, higher canopies, greater variability in tree size and more diverse vertical structure than do younger forests (Bingham and Sawyer, 1991; Carey *et al.*, 1991; Huff *et al.*, 1991; Spies and Franklin, 1991).

All these structural characteristics have been shown to be related to patterns of avian distribution. Thompson and Capen (1988) found that canopy height and volume, understory density, tree diameter, number of snags and basal area of deciduous and coniferous trees best explained the variation in bird distribution among forest seral stages. Avian community patterns have been related to the vertical profile of vegetation (Karr and Roth, 1971; Wiens, 1973; Rov, 1975; Nilsson, 1979; Rotenberry *et al.*, 1979; Roth, 1979) and horizontal foliage diversity (Wiens, 1974; Willson, 1974; Roth, 1976). James (1971) found percent canopy cover, canopy height and number of tree species per unit area explained the most variance in habitat differences among bird species. Species richness was highly correlated with mean basal area (Gerell, 1988, Nilsson, 1979, Osborne, 1984, Braithwaite *et al.*, 1989) and bird abundance with spatial heterogeneity (Gerell, 1988). The importance of snags for foraging and nesting-cavities has been demonstrated for many bird species (e.g. Bull, 1978; Bull and Meslow, 1977; Mannan *et al.*, 1980) and the abundance of cavity nesters has been correlated with the abundance of snags (Thomas *et al.*, 1979; Mannan *et al.*, 1980).

These habitat characteristics have also been related to the occurrence of individual species. For example, Spotted Owl abundance is related to high vertical canopy layering and snag diameter (Mills *et al.*, 1993). The abundance of Vaux's swift is correlated with density of large snags and large trees (Lundquist and Mariani, 1991).

We have shown that eastern old-growth pine forests also have distinguishing structural characteristics (Chapter 1). Old-growth pine forests had significantly more layers of vegetation, greater spatial variability in the number of vegetation layers, a taller canopy, more canopy cover and greater tree species richness in the upper canopy, than mature or managed forests. However, the extent to which these structural differences influence the abundance of bird species is unknown.

In this study, we compare the abundance of six selected bird species in old-growth pine forests, mature pine forests and managed forests in the Temagami region of northern Ontario, and relate abundances to specific habitat features.

The intent of the study was not to provide a complete characterization of these species' habitat requirements, but rather to test if the documented differences in habitat structure among forest-types influence their abundance (consequently, only certain habitat gradients were measured).

METHODS

The study area is described in Chapter 1.

DESCRIPTION OF FOREST-TYPES

Old-growth stands are those that have developed over a long period free of catastrophic disturbances (Franklin *et al.*, 1981). We define catastrophic as any disturbance that results in changing the dominant tree species in a stand.

In this study, old-growth and mature stands are both pine-dominated. Old-growth stands have no history of catastrophic disturbance for at least 150 years, and mature stands for approximately 100 years.

Managed stands were previously dominated by pine (aerial photographs, circa 1940). The pine was selectively logged roughly 50 years ago (i.e. the pine stand was catastrophically disturbed). The understory trees have now matured, so that these stands represent recently-disturbed forests in which the oldest trees (principally Eastern White Cedar (*Thuja occidentalis*) are nevertheless similar in age to those in mature or old-growth stands.

SITE SELECTION

Study sites were selected using information from the 1980 Forest Resource Inventory (FRI) data (Ontario Ministry of Natural Resources, based on 1977 aerial photography). This inventory of forested regions is carried out periodically to provide information on forest composition. Using aerial photographs, maps are produced which delineate forest stands: areas of forest dominated by similar vegetation. An estimate of the percent cover the dominant tree species in the stand is provided, along with an estimate of average stand height, average stand age, stand area and site class (OMNR, 1992a; 1992b). Site class is a numerical expression of productivity, determined using Normal Yield Tables. There are five site classes: X, 1, 2, 3 and 4 with 'X' being the highest site quality and '4' the poorest site quality (OMNR, 1992b).

Twenty-nine sites were sampled (Appendix A.1). Only one site was located in most FRI stands; seven stands contained two study sites each. These sites were separated by at least 500 m and were considered to be independent samples. There was no strong bias in site class among forest types, although managed stands had slightly poorer site conditions in general (i.e. more class '3' stands) (Appendix A.2).

Ten sites were classified as old-growth, nine as mature, and ten as managed forests (Appendix A.1). The FRI stand-age estimate was used as an indication of time since catastrophic disturbance for pine sites (i.e. the age of the dominant trees in the stand indicates that the pine stand has developed without catastrophic disturbance for at least that length of time).

Managed stands were selected with the advice of the Ontario Ministry of Natural Resources, Temagami District, based on knowledge of previous logging activities. Logging in the stands was verified by the presence of stumps, now rotted, and by evidence of old logging-roads, remnants of machinery and paint blazes on trees. Some large pines remain in managed stands along lake shorelines, as well as the occasional pine tree in the forest interior; these often bore a paint mark, probably indicating that they were not logged due to their size at the time or a "defect" (e.g. crooked trunk).

STUDY DESIGN

A 1-kilometer transect was laid out at each study site, 100 m from any edge. Five bird survey points were established along this transect. The first point was located 200 m from the edge of the stand, and each subsequent point was located at 200-meter intervals.

SPECIES SELECTION

Birds were selected for several reasons. The conservation of songbirds is highly valued by the Canadian public; a greater percentage of Canadians surveyed valued the conservation of birds other than waterfowl, over waterfowl and mammals (Filion *et al.*, 1993). There is concern that forest-cutting may have a negative impact on bird populations. Some neotropical migrants have shown population declines, which may be related to the effects of forest cutting and fragmentation (Robbins, 1979; Whitcomb et *al.*, 1979; Terborgh, 1992). Birds are relatively easy to census compared to other wildlife species. Birds are an important component in the health of forest ecosystems, for example, in their role as insectivores (e.g spruce budworm regulation) (Holmes, 1990). And finally, previous work on the autecology of the species selected suggests that their abundances may be correlated with the habitat features that distinguish old-growth forests.

Eight bird species were censused at each site. Four of the species are expected to be associated with features of late-seral coniferous habitat: Blackburnian Warbler (*Dendroica fusca*), Black-throated Green Warbler (*Dendroica virens*), Pine Warbler (*Dendroica pinus*), and Solitary Vireo (*Vireo solitarius*). These warbler species make extensive use of large conifers, and they often nest and forage in the upper canopy (Crins, 1988; Eagles, 1988). The Black-throated Green Warbler is one of the most common and constant of warblers occurring in evergreen needle-leaved forests, although it also breeds in deciduous forests (Kendeigh, 1948). The Blackburnian Warbler is also characteristic of evergreen needle-leaved forests (Kendeigh, 1948). The breeding habitat of the Pine Warbler is restricted to open pine woods (Kendeigh, 1948; Bent, 1953).

It typically feeds in the upper canopy (Anderson and Shugart, 1974). Salzman (1971) contends that Pine Warblers are very sensitive to habitat disturbance. The Solitary Vireo, a foliage gleaner, is also typical of northern coniferous woods, and is found most often in habitats with continuous canopy (James, 1988).

Since the Black-and-White Warbler (*Mniotilta varia)* is a bark-gleaner, large trees with deeply-furrowed bark may be an important habitat feature, as suggested for other bark-gleaners in the Pacific North-west (Carey *et al.*, 1991). This species is associated with mixed-woods with some deciduous component (Cartwright, 1988). It feeds by gleaning insects from the trunks and large limbs of trees (Bent, 1953).

Three other species, not expected to be strongly associated with old-growth habitat, were also censused for the sake of comparison. The Swainson's Thrush (*Hylocichla ustulata*) is also a species of coniferous forests but prefers nesting in early to mid-successional stages (Meslow and Wight, 1975) with dense understory (Bent, 1964; Mannan, 1977; Sadler, 1988). The other species censused are typically associated with more disturbed mixed-woods with some deciduous habitat component, typical of the managed sites. The Black-throated Blue Warbler (*Dendroica caerulescens*), a shrub foliage gleaner, nests and forages in lower strata of the forest (Black, 1975; Holmes *et al.*, 1979). It will nest in second-growth forests and selectively-logged areas, provided that the canopy remains intact (Fraser, 1988). The Veery (*Hylocichla fuscescens*) is frequently found in disturbed forests with bushy undergrowth (Sadler, 1988).

BIRD SURVEYS

Bird surveys were conducted in June, 1992 using a modified version of the point-count method with unlimited distance (Blondel *et al.*, 1981). Sites were only visited once during the breeding season. At each survey point, the number of different males heard singing during a period of 10 minutes was recorded.

All auditory censuses suffer from confounding factors including variation in song attenuation and emission frequency, behavioural differences among species, observer bias, habitat structure, season, time of day and weather (Shields, 1979). These factors were minimimized as much as possible. Data were collected by only two observers. All surveys were conducted between 6h00 and 11h00 in good weather. Visits to the different forest types (i.e. old-growth, mature, managed) were alternated between observers to reduce observer bias and were staggered temporally to avoid seasonal bias among treatments as the breeding season progressed. Each species was analysed separately, eliminating comparative problems due to differences in singing behaviour among species.

ANALYSIS OF BIRD CENSUS DATA

Census results for a particular site were summed over the five counting stations in each site. At three sites, the counts were based on 4, rather than 5, sampling points due to constraints of site features (cliffs, bogs, etc). For these sites, the summed count was multiplied by 1.25 to correct for sampling intensity.

To test if bird abundances differed among forest-types, the abundance of each bird species in old-growth, mature and managed sites was compared using one-way ANOVA, or if the assumptions of a parametric test could not be not met, the Kruskal-Wallis non-parametric ANOVA. Accordingly, plots of species abundance will show means for species analyzed parametrically, and medians when non-parametric tests were used.

Normality of residuals was tested using Lilliefor's test, and Bartlett's test was used to test for homoscedasticity (Appendix A.2). Power was calculated for non-significant parametric tests (Appendix A.3). The Mann-Whitney U-test, corrected for multiple comparisons, was used for *a posteriori* comparisons of Kruskal-Wallis results. *A posteriori* comparisons of ANOVA results were done using Tukey tests.

MEASUREMENT AND ANALYSIS OF VEGETATION DATA

A number of vegetation characteristics were measured at each site (Table 1). Vegetation was sampled along the transect established for point-counts during the summers of 1991 and 1992. Sampling began 100 m before the first bird-survey point and extended 100 m beyond the last bird-survey point. In addition, vegetation was sampled for 50-meters on either side of each bird survey point, perpendicular to the main transect.

Tree density was measured using a modified point-distance nearest-neighbour technique (Batchelor, 1973). Every 10 meters along both the main and cross-transects, the distance from the observer to the nearest stem (diameter>10 cm) was recorded, as well as tree species and diameter at breast height (dbh). This procedure was repeated to the first stem's "nearest neighbour", and to the second stem's "nearest neighbour". Total stem density, and density by species was calculated for each stand according to Batchelor (1973). Non-pine coniferous tree species were grouped, as were deciduous shade-tolerant (birch, aspen) and deciduous shade-intolerant (maple, ash, oak) tree species.

Since large trees are thought to be an important distinguishing characteristic of old-growth forests, tree densities were calculated for three size-classes: small (10-20 cm dbh), medium (21-50 cm dbh), and large (over 50 cm dbh). Mature Eastern White Pine (*Pinus strobus*) commonly attains a diameter of 60-150 cm, and Red Pine (*Pinus resinosa*) between 60-90 cm (Grimm, 1983), depending on site conditions. The largest White Pine and Red Pine sampled in this study measured 94 cm dbh, and 70 cm dbh respectively.

Vegetation cover in each of several strata (0 to 1 m, 1 to 8 m, 8 to 15 m and over 15 metres) was measured every 15 m along the transects. This involved recording the species of trees and shrubs in each stratum which intercepted an imaginary line that started at the ground and extended upward through the canopy. The presence/absence of vegetation in a given layer at each sampling point were summed for each stand and used to calculate percent cover per layer (the number of occurrences of foliage divided by the total number of points measured), the average number of tree and shrub species occurring in each layer, the average number of layers per stand with vegetation cover, and the variance in the number of layers (calculated among sampling points in a site). Percent cover and the average number of vegetation layers were interpreted as indices of the vertical structure of the forest. The variability in the number of layers was interpreted as an index of the amount of spatial variability in vertical structure, while number of tree and shrub species is an index of vegetation diversity.

BIRD-VEGETATION RELATIONSHIPS

Spearman Rank Correlations (or Pearson correlations, in the case of Pine Warbler) were calculated to identify relationships between vegetation characteristics and abundance of each bird species. Since many of the descriptors of forest structure may be related (e.g. height, age and density of large trees in a stand), Spearman Rank Correlations were also calculated among the vegetation variables, to determine to what extent they were colinear (colinearity was defined as a significant correlation at $p<0.05$).

When the abundance of a bird species was significantly correlated with more than one vegetation variable, multiple regressions were performed. Bivariate plots of abundance as a function of vegetation variables were first examined for evidence of non-linear relationships. When pairs of vegetation variables were strongly colinear, only the one most highly correlated with bird abundance was included in the regression model.

We also wished to test the hypothesis that the differences in bird abundance among forest-types could be related to differences in vegetation structure among forest-types. To do this, we did an ANCOVA in which the vegetation variables selected in the multiple regression were used as covariates, and forest-types as treatments.

Table 1- Measures of vegetation structure and composition in old-growth, mature and managed forests.
(Density (stems/hectare); Height (meters)).

Total tree density
Density of trees in three size classes (10-20 cm, 20-50 cm, over 50 cm dbh)
Density of pine, non-pine conifer, deciduous-shade tolerant, deciduous shade intolerant trees (also by size class)
Total snag density
Snag density in three size classes (10-20 cm, 20-50 cm, over 50 cm dbh)
Stand height
Average number of vegetation layers per stand
Variance in number of vegetation layers per stand
Number of tree and shrub species per layer (0-1 m, 1-8 m, 8-15 m, over 15 m)
Vegetation cover per layer (0-1 m, 1-8 m, 8-15 m, over 15 m)

RESULTS

Bird Abundance

Bird abundance did not differ significantly among forest types (i.e. old-growth, mature, managed) for most of the species studied. Abundances of Veery, Swainson's Thrush, Black-throated Blue Warbler and Black-and-White Warbler were indistinguishable among old-growth, mature and managed stands (Figs. 5-8; Table 2). Veery abundance was very low in all three forest types (Fig. 8).

The abundances of Solitary Vireo, Black-throated Green and Blackburnian Warblers did not differ significantly between old-growth and mature, or between mature and managed stands. Differences in abundance between old-growth and managed stands approached significance ($0.05<p<0.10$) (Figs. 2-4; Table 2). Forest type explained only 16% of the variance in abundances of these species (Table 2).

Pine Warbler was the only species that differed significantly among forest types. It was more abundant in old-growth and mature than in managed stands (i.e. higher in pine than non-pine forest) (Fig. 1; Table 2).

Relationship of Bird Abudance and Measured Habitat Variables

Abundances of most of the species censused showed few significant relationships with habitat characteristics (Table 3). Black-and-White Warbler abundance was weakly negatively correlated with percent ground cover. Black-throated Blue Warbler abundance was weakly positively correlated with the density of medium deciduous shade-tolerant trees. In linear regression models, stand height explained 15% of the variance in Blackburnian Warbler abundance, and average number of vegetation layers explained 24% of the variance in Black-throated Green Warbler abundance (Table 7; Table 9). Solitary Vireo abundance was positively correlated with the density of large pine, and negatively correlated with the density of small non-pine conifers. In a multiple regression, only density of large pine was significant, explaining 18% of the variance in Solitary Vireo abundance (Table 11).

Pine Warbler abundance, on the other hand, was significantly correlated with many vegetation characteristics (Table 4). After eliminating colinear variables, the best predictors of Pine Warbler abundance in a multiple-regression model were number of trees species in the 8 to 15 m layer, canopy height and density of medium-sized pine (Table 5).

The Relationship of Bird Abundance with Forest Type

Black-and-White and Black-throated Blue Warblers were significantly related to habitat characteristics, but not to forest type. Blackburnian Warbler abundance was similarily predicted by stand height and forest type (r^2=0.15; $F_{1,27}$=5.827 and r_2=0.16; $F_{1,27}$=3.15, respectively). The abundances of Black-throated Green Warbler and Solitary Vireo were more strongly predicted by habitat variables than by forest type. A direct comparison for Pine Warbler is not possible since the Kruskal-Wallis test provides no correlation coefficient.

For those species that differed among old-growth, mature and managed forests, we wished to determine whether additional variance could be explained by forest type after controlling for vegetation variables. Forest type did not explain any additional residual variance in abundances of Pine Warbler, Black-throated Green Warbler, Solitary Vireo and Blackburnian Warbler after accounting for the variance explained by significantly-related vegetation characteristics (Tables 5-12).

Figure 1- Pine Warbler abundances in 10 old-growth, 9 mature and 10 managed sites. The box represents the range between the 25th and 75th percentiles of the data; the horizontal line within the box marks the value of the 50th percentile. Capped bars indicated the 10th and 90th percentile points.

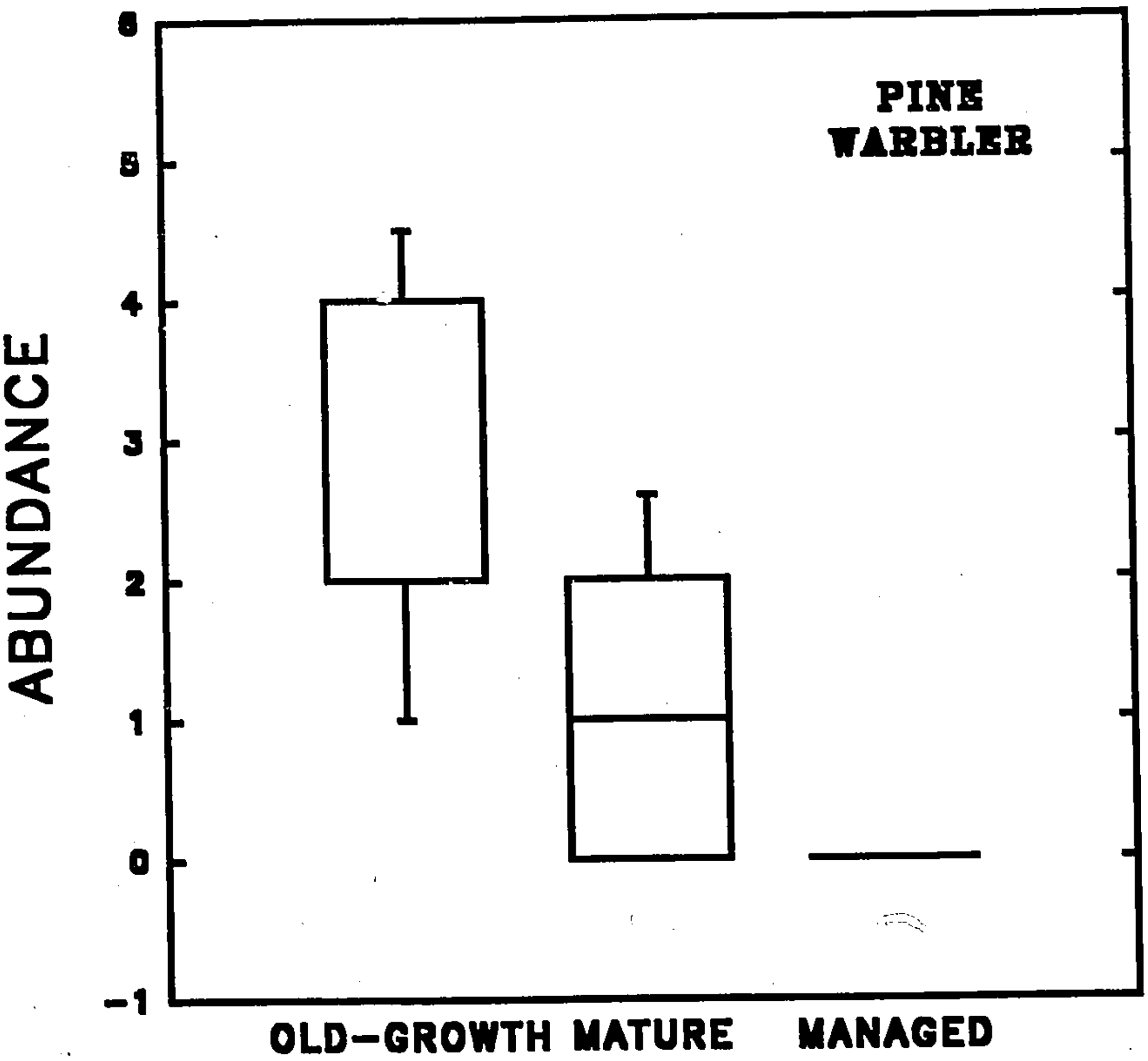
PINE
WARBLER
ABUNDANCE
6
5
4
3
2
1
0
-1
OLD-GROWTH
MATURE
MANAGED

Figure 2- Mean abundance of Solitary Vireo ± 1 standard error.

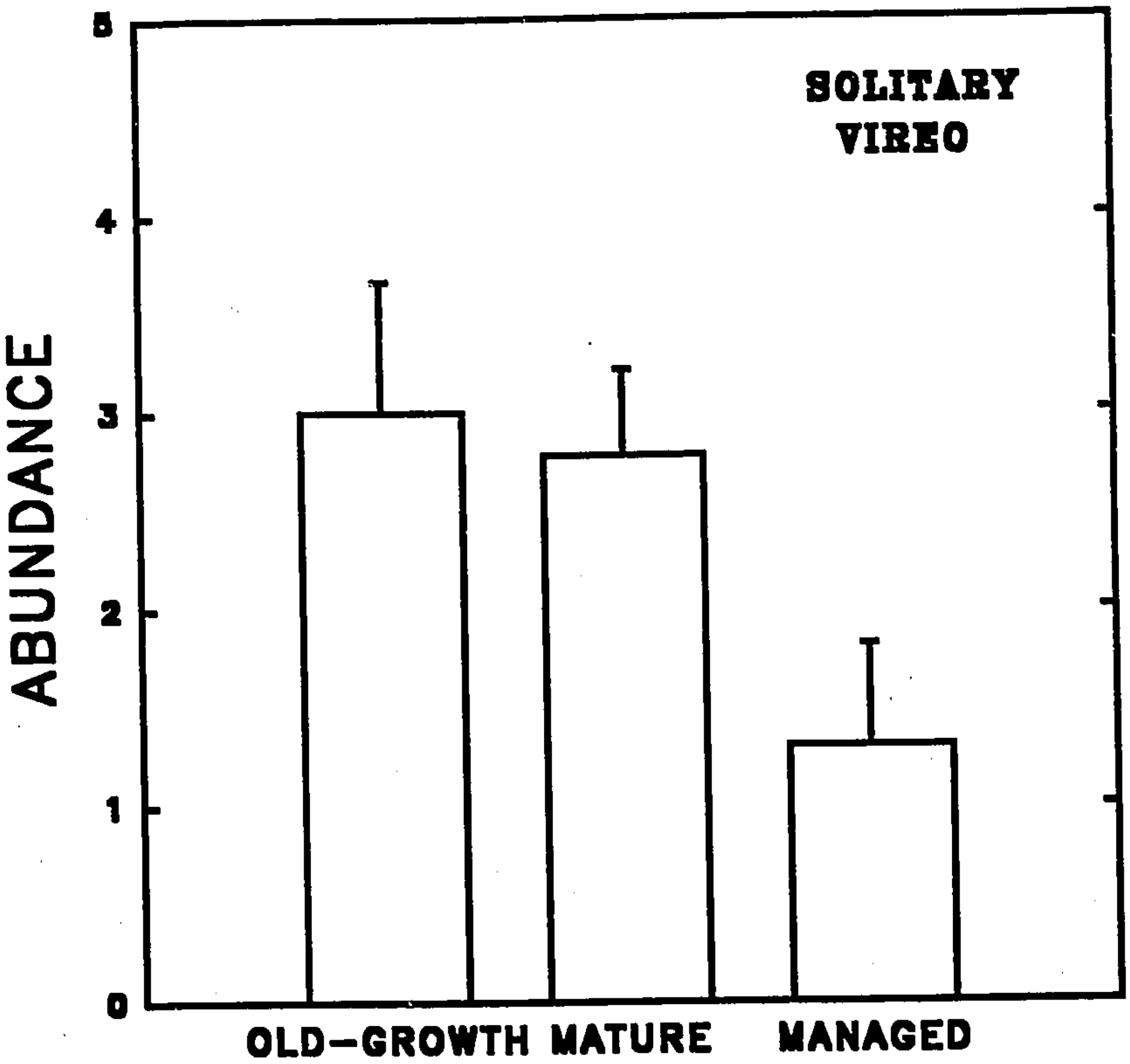
SOLITARY
VIREO
ABUNDANCE
0
1
2
3
4
5
OLD-GROWTH
MATURE
MANAGED

Figure 3- Mean abundance of Black-throated Green Warbler ± 1 standard error.

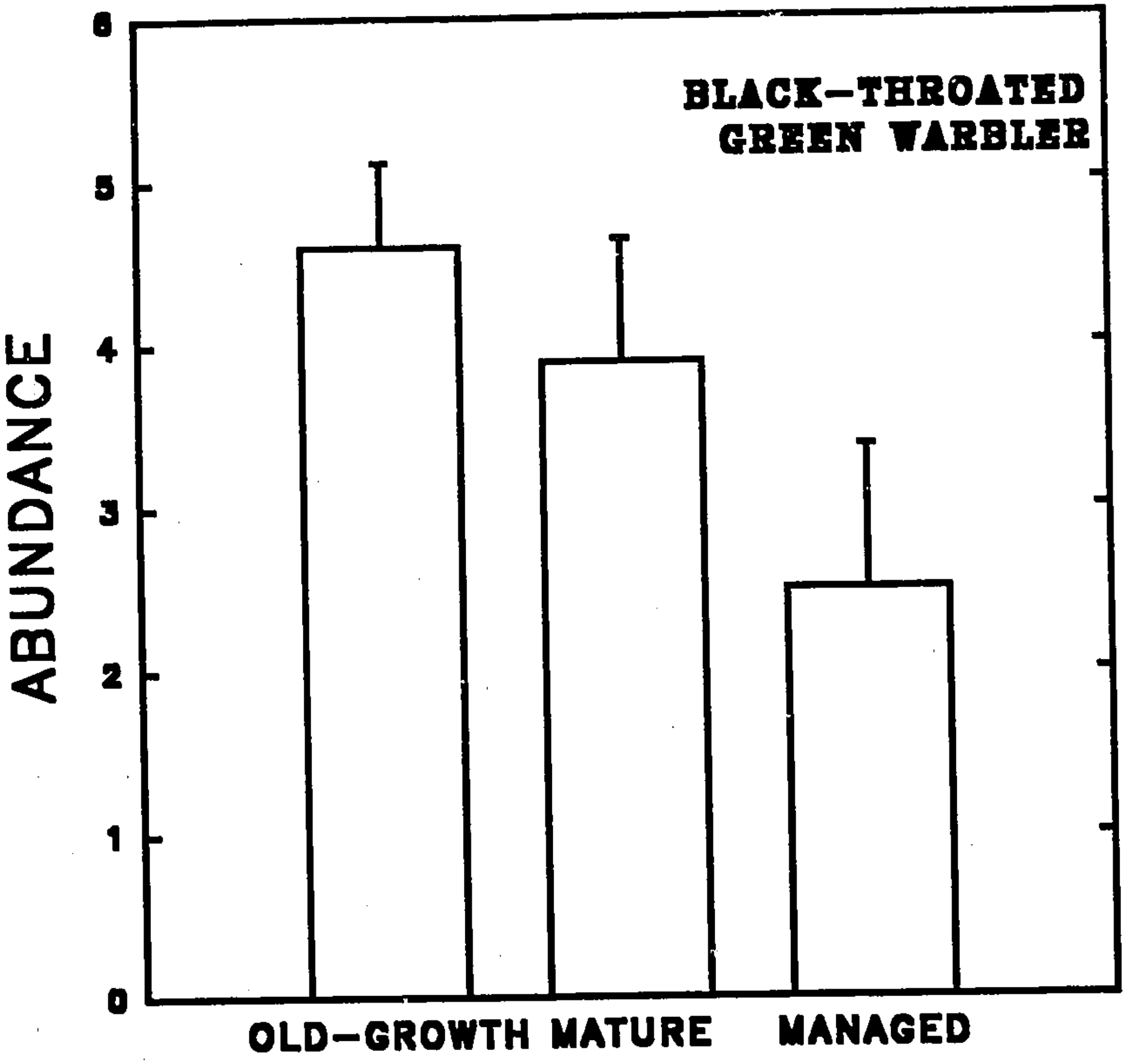
BLACK-THROATED
GREEN WARBLER
ABUNDANCE
6
5
4
3
2
1
0
OLD-GROWTH
MATURE
MANAGED

Figure 4- Mean abundance of Blackburnian Warbler ± 1 standard error.

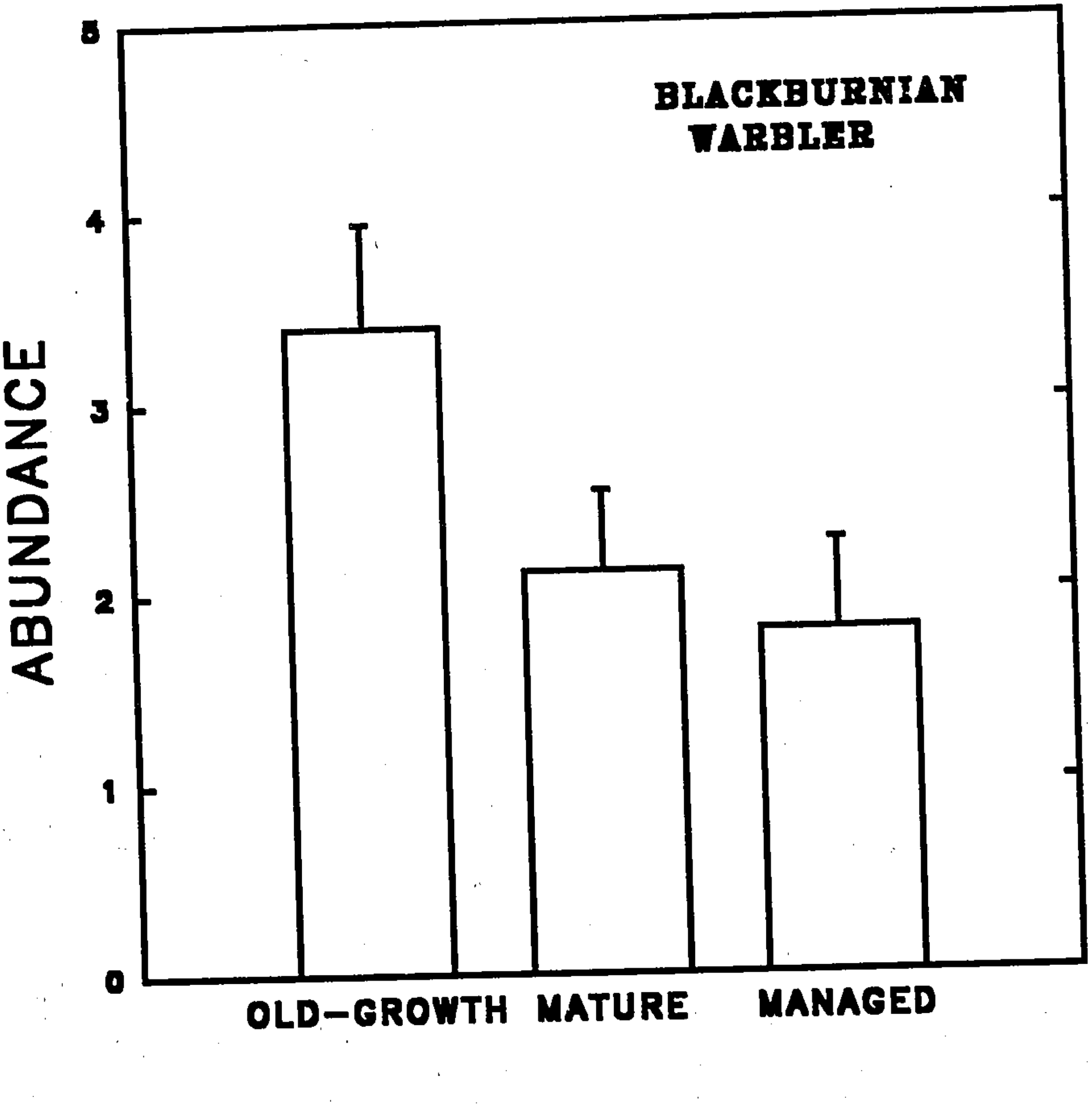
BLACKBURNIAN WARBLER
ABUNDANCE
0
1
2
3
4
5
OLD-GROWTH
MATURE
MANAGED

Figure 5- Black-throated Blue Warbler abundances in 10 old-growth, 9 mature and 10 managed sites. The box represents the range between the 25th and 75th percentiles of the data; the horizontal line within the box marks the value of the 50th percentile. Capped bars indicated the 10th and 90th percentile points.

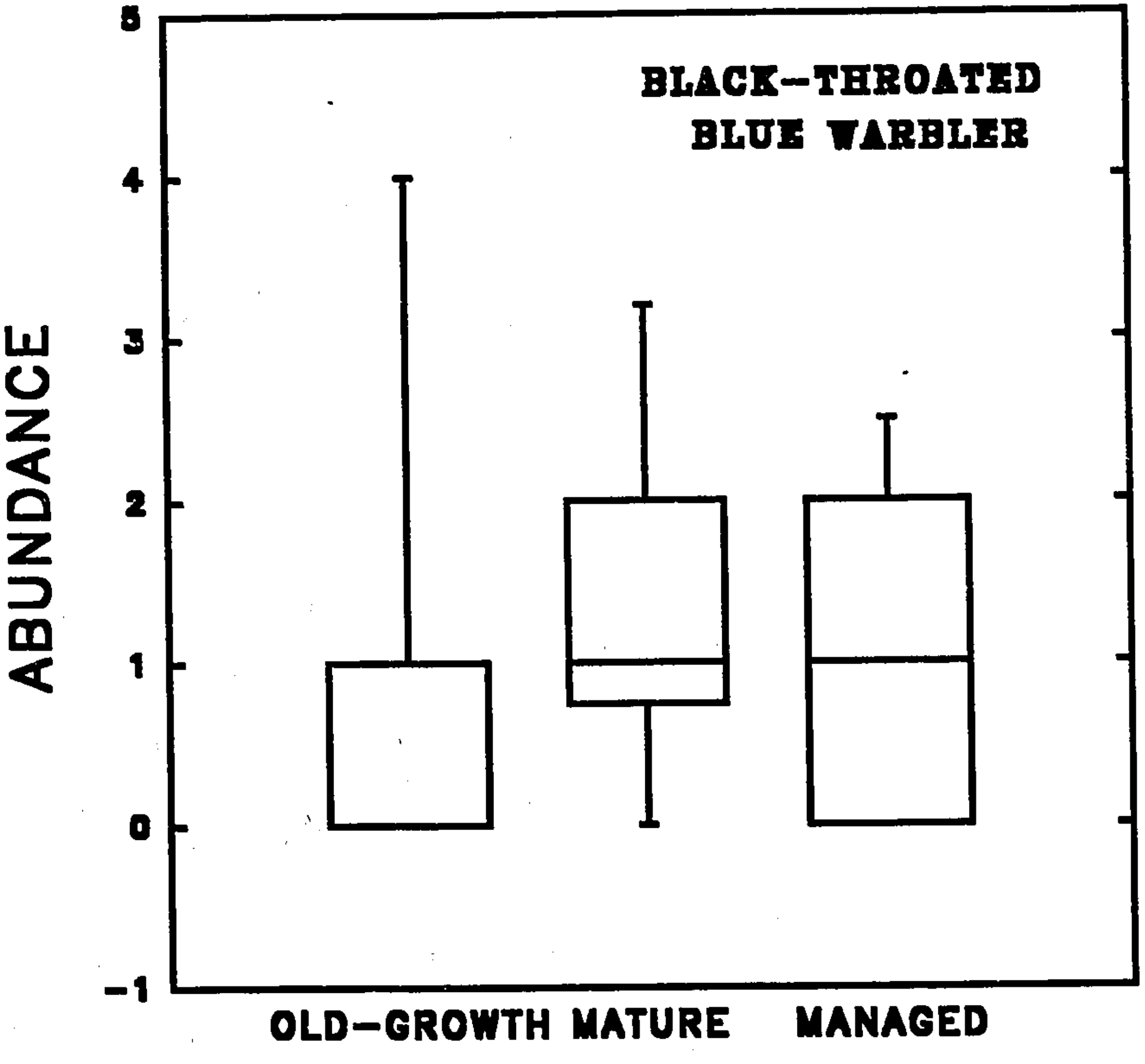
BLACK-THROATED
BLUE WARBLER
ABUNDANCE
5
4
3
2
1
0
-1
OLD-GROWTH
MATURE
MANAGED

Figure 6- Mean abundance of Black-and-White Warbler ± 1 standard error.

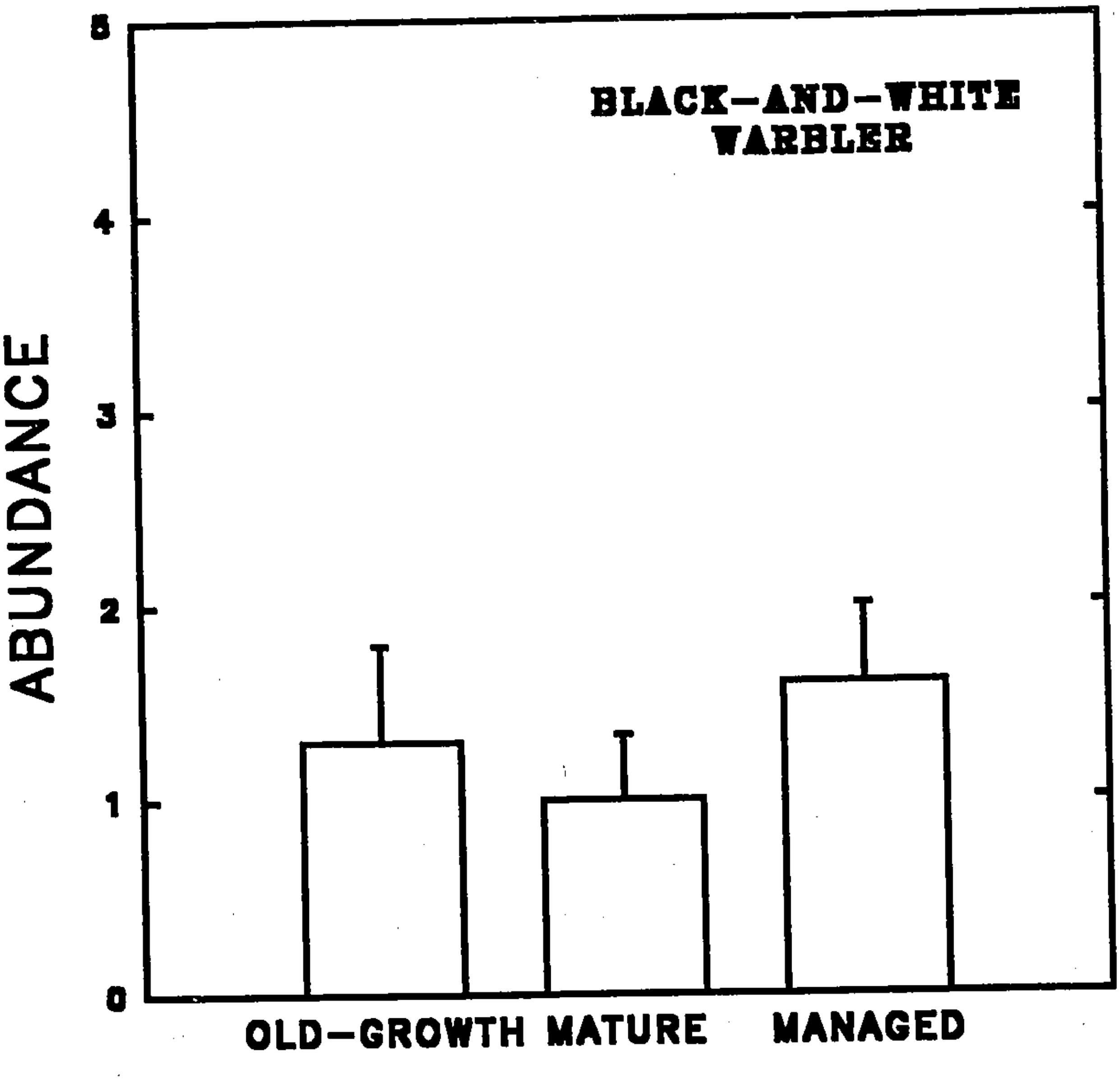
BLACK-AND-WHITE WARBLER
ABUNDANCE
5
4
3
2
1
0
OLD-GROWTH
MATURE
MANAGED

Figure 7- Swainson's Thrush abundances in 10 old-growth, 9 mature and 10 managed sites. The box represents the range between the 25th and 75th percentiles of the data. The horizontal line within the box marks the value of the 50th percentile (for mature sites, the 50th percentile equates the 25th percentile). Capped bars indicated the 10th and 90th percentile points.

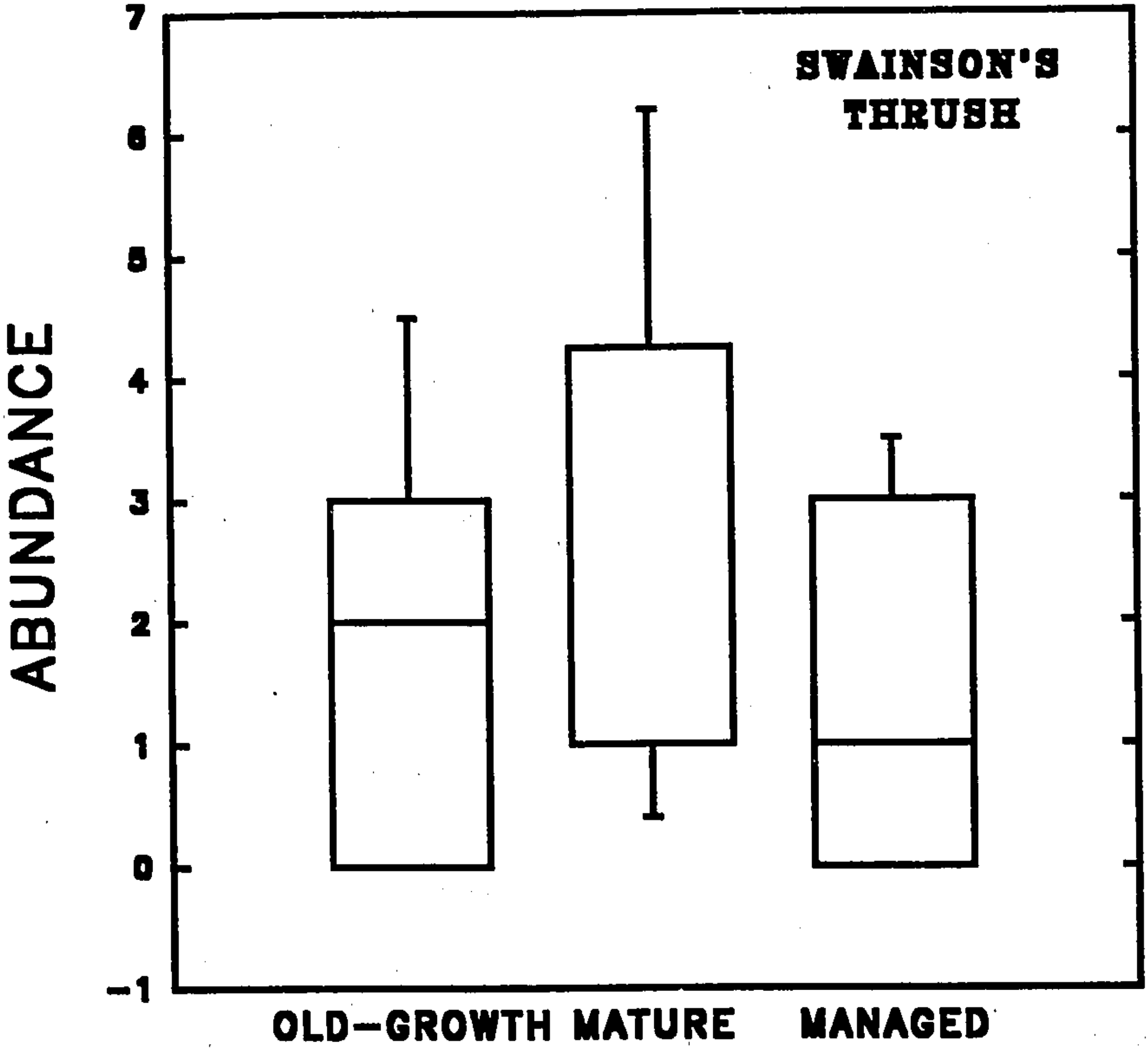
SWAINSON'S
THRUSH
ABUNDANCE
7
6
5
4
3
2
1
0
-1
OLD-GROWTH
MATURE
MANAGED

Figure 8- Veery abundances in 10 old-growth, 9 mature and 10 managed sites. The box represents the range between the 25th and 75th percentiles of the data; the horizontal line within the box marks the value of the 50th percentile. Capped bars indicated the 10th and 90th percentile points.

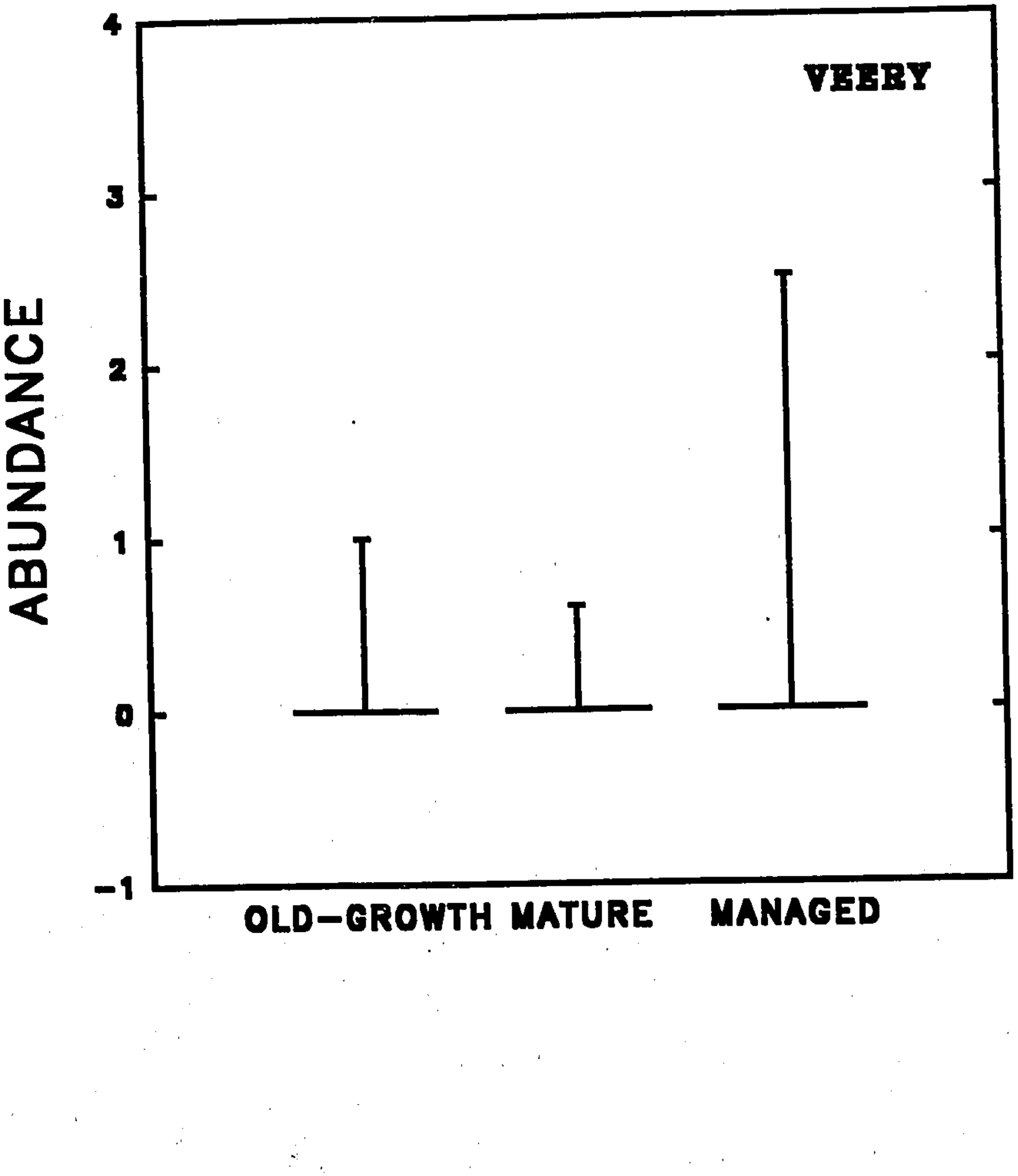
VEERY
ABUNDANCE
4
3
2
1
0
-1
OLD-GROWTH
MATURE
MANAGED

Table 2- Results of One-Way ANOVA and Kruskal-Wallis tests comparing bird abundances among forest-types (old-growth (og), mature (mt), managed (mn)). N=29.
n.a.= not applicable

Species	Test	F	P	r^2	*A Posteriori* Comparison
Pine Warbler	K-W	21.89	0.000	-	og=mt>mn**
Blackburnian Warbler	AOV	3.15	0.059	0.16	og>mn;og=mt; mn=mt*
Black-and-white Warbler	AOV	0.50	0.613	-	n.a.
Black-throated Blue Warbler	K-W	0.53	0.576	-	n.a.
Black-throated Green Warbler	AOV	2.21	0.070	0.16	og>mn;og=mt; mn=mt*
Swainson's Thrush	K-W	0.52	0.582	-	n.a.
Solitary Vireo	AOV	2.83	0.077	0.16	og>mn;og=mt; mn=mt*
Veery	K-W	0.00	0.999	-	n.a.

** significant at $p<0.05$
* significant at $p<0.10$

Table 3- Summary of significant (p>0.05) Spearman rank[a] or Pearson[b] correlations between bird species abundances and vegetation characteristics. Tree density (stems/hectare); stand height (meters); stand age (years). (N=29)

Bird Species	Vegetation Characteristic	r	P
Black-throated Green Warbler	No. of layers[1]	0.518[b]	0.004
Blackburnian Warbler	Stand height[1]	0.421[b]	0.022
Solitary Vireo	Density of large pines	0.458[b]	0.010
	Density of small non-pine conifers	-0.402[b]	0.030
Black-and-White Warbler	No. of species in 0-1 m layer	-0.375[a]	0.045
Black-throated Blue Warbler	Density of medium deciduous shade-tolerant trees	0.478[a]	0.009

[1] Characteristics that are significantly higher in old-growth, than in managed or mature forests (Chapter 1).

Table 4- Pearson Correlations between Pine Warbler abundance (transformed as $(x+0.5)^{1/2}$) and all significantly ($p>0.05$) correlated vegetation characteristics in 29 forest stands. Density (snags/hectare); Stand height (meters); Stand age (years).

Vegetation Characteristic	r	P
No. of species in 8-15 m layer[1]	0.592	0.001
Average stand height[1]	0.579	0.001
Variance in the number of layers[1]	0.564	0.001
Percent cover in over 15 m layer[1]	0.554	0.002
No. of species in over 15 m layer[1]	0.533	0.003
Density of medium non-pine conifers	-0.527	0.003
Average stand age[1]	0.525	0.003
Percent cover in 0-1 m layer	-0.510	0.005
Density of small non-pine conifers	-0.509	0.005
Density of medium pine	0.489	0.007
Density of small pine	0.443	0.016
Average number of layers[1]	0.430	0.019
Density of large pine	0.378	0.043

[1] Characteristics that are significantly higher in old-growth than in mature or managed stands (Chapter 1).

Table 5- Multiple regression analysis examining the effect of number of vegetation species in the 8 to 15 m canopy layer (SP8TO15), the density of medium-sized pine (DENPINM) (20-50 cm diameter at breast height) (stems/hectare) and canopy height (HEIGHT) (meters) on Pine Warbler abundance in 29 forest stands.

Dependent variable:sqrt(Pine Warbler abundance) r^2= 0.70

SOURCE	COEFFICIENT		STD ERR	STD COEF	P
CONSTANT	-0.581		0.243	0.000	0.025
SP8TO15	0.130		0.029	0.496	0.000
DENPINM	0.002		0.000	0.452	0.000
HEIGHT	0.034		0.010	0.373	0.002
SOURCE	SS	MS	DF	F-RATIO	P
REGRESSION	5.86	1.955	3	22.63	0.000
RESIDUAL	2.16	0.086	25		

Table 6- ANCOVA examining the effects of density of medium pine (DENPINM), stand height (HEIGHT) and number of species in the 8 to 15 m layer (SP8TO15) on Pine Warbler abundance with forest-type (Treatment) as the categorical variable.

Dependent Variable: sqrt(Pine Warbler abundance) r^2=0.77

SOURCE	SS	MS	F	DF	P
Treatment	0.290	0.145	1.785	2	0.190
DENPINM	0.579	0.579	7.121	1	0.014
HEIGHT	0.087	0.087	1.076	1	0.310
SP8TO15	0.917	0.917	11.285	1	0.003
Error	1.87	0.081		23	

Table 7- Linear regression analysis examining the effect of average number of layers (LAYERS) on Black-throated Green Warbler abundance in 29 forest stands.

Dependent variable: Black-throated Green Warbler abundance r^2= 0.24

SOURCE	COEFFICIENT		STD ERR	STD COEF	P
CONSTANT	-0.554		0.800	0.000	0.494
LAYERS	0.930		0.296	0.518	0.004
SOURCE	SS	MS	DF	F-RATIO	P
REGRESSION	3.12	3.12	1	9.876	0.004
RESIDUAL	8.53	0.316	27		

Table 8- ANCOVA examining the effects of average number of layers (LAYERS) on Black-throated Green Warbler abundance with forest-type (Treatment) as the categorical variable.

Dependent Variable: Black-throated Green Warbler abundance r^2=0.28

SOURCE	SS	MS	F	DF	P
Treatment	0.327	0.164	0.499	2	0.613
LAYERS	1.290	1.290	3.931	1	0.058
Error	8.202	0.328		25	

Table 9- Linear regression analysis examining the effect of Forest Resource Inventory stand height estimate (HEIGHT)(meters) on Blackburnian Warbler abundance in 29 forest stands.

Dependent variable: Blackburnian Warbler abundance $r^2=0.15$

SOURCE	COEFFICIENT		STD ERR	STD COEF	P
CONSTANT	0.088		1.016	0.000	0.931
HEIGHT	0.117		0.049	0.421	0.023
SOURCE	**SS**	**MS**	**DF**	**F-RATIO**	**P**
REGRESSION	12.989	12.989	1	5.827	0.023
RESIDUAL	60.183	2.229	27		

Table 10- ANCOVA examining the effects of Forest Resource Inventory stand height estimate (meters) on Blackburnian Warbler abundance with forest-type (Treatment) as the categorical variable.

Dependent Variable: Blackburnian Warbler abundance $r^2=0.16$

SOURCE	SS	MS	F	DF	P
Treatment	2.596	1.298	0.563	2	0.576
HEIGHT	1.301	1.301	0.565	1	0.459
Error	57.588	2.304		25	

Table 11- Linear regression analysis examining the effect of density of large pine (DENPINL) on Solitary Vireo abundance in 29 forest stands.

Dependent variable: Solitary Vireo abundance $r^2 = 0.18$

SOURCE	COEFFICIENT		STD ERR	STD COEF	P
CONSTANT	1.785		0.373	0.000	0.000
DENPINL	0.020		0.008	0.458	0.013
SOURCE	SS	MS	DF	F-RATIO	P
REGRESSION	19.804	19.804	1	7.153	0.013
RESIDUAL	79.748	2.768	27		

Table 12- ANCOVA examining the effects of density of large pine (DENPINL) on Solitary Vireo abundance with forest-type (Treatment) as the categorical variable.

Dependent Variable: Solitary Vireo abundance $r^2=0.25$

SOURCE	SS	MS	F	DF	P
Treatment	6.820	3.410	1.255	2	0.302
DENPINL	9.728	9.728	3.580	1	0.070
Error	67.928	2.717		25	

DISCUSSION

Bird abundances were more strongly related to structural and floristic characteristics of habitat than to forest type. The abundances of five species were significantly correlated with some measured aspects of habitat structure, while four species were significantly correlated to floristic features, and only one to forest type. Moreover, the correlation with forest-type in the latter case apparently reflects colinearity between forest-type and vegetation characteristics.

Habitat associations described in this study are similar to those reported elsewhere. The relationship of Pine Warbler abundance to pine dominance, percent canopy cover, canopy height, shrub species diversity, large tree density, small trees in the lower canopy, and moderate coniferous cover has been reported in Tennessee, Maine and Minnesota, and Maryland (Anderson and Shugart, 1974; Collins, 1983; Lynch and Whigham, 1984). Kerlinger and Doremus (1981) measured Pine Warbler abundance in three pine barrens in New York that varied in the amount of disturbance: populations were locally extirpated from the most disturbed site and present in significantly lower numbers in all seral stages of the sites intermediate in disturbance, compared to undisturbed sites.

The abundance of Black-throated Green Warblers is not strongly related to floristics. Rather, they have been reported from a variety of plant-community types (Brooks, 1940; Bent, 1953) including pine forests (Collins *et al.*, 1982), deciduous vegetation (Maurer and Whitmore, 1981) and spruce-fir forests (MacArthur, 1958). However, as in the present study, the abundance of this species has been related to multi-layered leaf arrangement (Horn, 1974; Holmes and Robinson, 1981), a relationship likely ensuing from its role as a foliage gleaner.

Martin (1960) found both Black-throated Green and Blackburnian Warblers in Algonquin Park, Ontario to be characteristic of late-seral coniferous habitat (Eastern Hemlock- *Tsuga canadensis*). Blackburnian Warblers were also found to occupy the canopy of pine forests. Blackburnian Warblers appear to occupy largely coniferous forests throughout their range (Noon *et al.*, 1980). Doerker and Earle (1992) characterized Blackburnian Warbler breeding habitat in Michigan as mesic coniferous forest with a high percent canopy closure.

Solitary Vireo abundance was related to density of large pine and oak, and canopy height in mixed conifer forest of the western Sierra Nevada (Morrison *et al.*, 1987). Black-throated Blue Warblers are largely deciduous-related species (Martin, 1960), as my results suggest. Abundances of this species are consistently correlated with shrub density (Darveau *et al.*, 1992; Steele, 1992; Steele, 1993), a gradient not measured in this study.

Our results for Black-and-White Warbler abundance are unclear. This species appears to exhibit geographic variation in habitat use across their range (Noon *et al.*, 1980). In Maine and Michigan, Black-and-White Warbler occupied open forest with high shrub density. In the central and southern part of its range, this species occupied forests with many large trees, well-developed canopies, and low shrub density (Noon *et al.*, 1980). I found a weak negative correlation with shrub density but no other correlations.

Measured habitat characteristics were generally weak predictors of species' abundances, with the exception of the Pine Warbler. Other studies have similarily shown that some bird species are distributed according to specific habitat variables, while distribution of other species is weakly related to a large number of variables (Anderson and Shugart, 1974). Several studies have shown that breeding birds generally exhibit broad habitat preferences (Cody, 1978; Rotenberry and Wiens, 1980; Collins *et al.*, 1982) which may contribute to the difficulty of producing accurate predictive generalizations (Collins, 1983). The highly adaptable nature of many species, particularily the wood warblers (Parulidae) is well documented (Morse, 1985). Species that occur in many successional stages do so either because they can occupy the same niche or due to their adaptability (Anderson et *al.*,1979). Some species have stereotyped foraging patterns requiring specific forms of habitat structure, while other species have a greater plasticity in habitat use thereby being able to live in a wider variety of habitats (Morse, 1971). The strong relationship of Pine Warbler abundance to the measured habitat variables is a demonstration of its habitat specificity.

MANAGEMENT IMPLICATIONS

Forest management directed primarily to timber production reduces tree basal area and forest canopy. Depending on the management regime, it may also change the dominant tree species in a stand. The measured habitat characteristics which distinguished old-growth, mature and managed forests were only weakly related to the abundance of most of the species censused. However, significant alterations to the amount of pine forest, and to canopy structure may have a strong adverse effect on Pine Warbler abundance.

Management for Pine Warblers will necessitate provision of late-successional pine forest habitat since tall canopies, an important habitat criterion, develop in older forests. This may entail conservation of existing forest stands or allowing future forest stands to develop on long rotational schedules (or both). Selective cutting may be an option if canopy cover is not greatly reduced. There is little information on the occurrence of Pine Warblers in plantations. Their relationship to species diversity in the upper canopy, and to multi-layered canopy structure suggest that monocultures would not provide optimal habitat.

The relative importance of old-growth, as compared to mature pine forest as Pine Warbler habitat is difficult to discern. Canopy height, variance in the average number of vegetation layers, number of species and percent cover in the upper canopy, average number of vegetation layers and stand age were all significantly higher in old-growth than in managed or mature stands (Chapter 1). All these characteristics were significantly correlated with Pine Warbler abundance. However, despite the observed difference in habitat characteristics between the two forest types, Pine Warbler abundance did not vary significantly between them. It is possible that the differences in abundance between the two stands may be too small to detect with the sample size used in this study.

Habitat-use patterns in one portion of a species' range may be of limited applicability with regard to habitat management throughout the entire range (Collins, 1983). While Noon *et al.* (1980) detected few cases of geographical variation in habitat use, Collins (1983) demonstrated that many warbler species were associated with different habitats in Maine and Minnesota. While this may be of true of species that are wide-ranging habitat generalists, the habitat characteristics related to Pine Warbler abundance seem to have wide-scale applicability. Similar abundance-habitat relationships were found in studies from Maryland, Maine, Minnesota and Tennessee (Anderson and Shugart, 1974; Collins, 1983; Lynch and Whigham, 1984).

LIMITATIONS OF THE STUDY

Abundance data collected over one breeding season provide no estimate of year-to-year variability in bird abundance. Breeding season studies are susceptible to unknown pre-breeding events. If overwinter survival is good, then populations may occupy a wider range of habitat in the spring, and if not, only a limited range of habitat may be used (Cody, 1981). This may alter the patterns of bird abundance among forest types. In high-density years, some birds may be forced into low-quality habitat. In low-density years some good habitat appears not to be selected since birds don't occupy all available habitat. As well, the quality of any habitat can change from year to year, making it important to monitor populations over a sufficiently long period to capture a broad range of the potential abundances (Venier *et al.*, 1993).

Although abundance data in this study was only collected over one breeding season, the habitat relationships observed are similar to other reported results. Further monitoring of these species would strengthen the conclusions concerning relative use of the three forest-types, particularly for those species where abundance patterns among forest-types approached significant differences.

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APPENDIX A.1- Forest stand descriptions from a 1980 forest resource inventory based on 1977 aerial photographs. Site No.=sampling site designation (MN=managed stands, OG=old-growth stands, MT=mature stands); Site Class[1]; FRI No.=stand designation for forest resource inventory[2]; Species Composition=proportion[3] of tree species[4] estimated from aerial photographs; Age (years)=estimate of age of dominant tree species from aerial photographs; Height (meters)=estimate of stand height from aerial photographs; Area (hectares).

Site No.	Site Class	FRI No.	Species Composition	Age	Ht.	Area
MN0	3	St38	Sb3Sw2B2Pw1Bw1Ce1	91	10	165
MN1	2	B46	Bw4Po3Sw2Ab1	111	20	81
MN2	3	B38	Sw2Sb1Pw2Ce2Bw1Mh1By1	173	19	210
MN3	2	D66	Sb6Sw2Bw1B1	101	14	155
MN4	2	J29	Bw5Po2Sw1Pr1Pw1	96	20	137
		J30	Bw4Po3Pj2Sb1	91	20	129
MN5	2	B46	Bw4Po3Sw2Ab1	111	19	81
MN6	3	B38	Sw2Sb1Pw2Ce2Bw1Mh1By1	173	14	210
MN7	2	J29	Bw5Po2Sw1Pr1Pw1	96	20	137
		J30	Bw4Po3Pj2Sb1	91	20	129
MN8	3	St80	Sb2Sw2Ce3Ab2Bw1	122	13	138
MN9	3	St38	Sb3Sw2B2Pw1Bw1Ce1	91	10	165
OG0	2	P72	Pw4Po1Bw1Ce1Pr1Sb1B1	196	30	66
OG1	3	P52	Pw4Mh2By2Ce1Bw1	226	22	185
OG2	2	P56	Pw6Mh2Pr1Ms1	203	30	255
		J84	Pw6Mh2Pr1Ms1	203	30	87
OG3	3	P65	Pr4Pw3Bw2Po1	156	19	127
OG4	1	V45	Pw6Bw1Po1Ms1B1	179	31	139
OG5	2	P44	Pr5Pw3Bw1Po1	153	23	140
OG6	2	S123	Pw4Pr2Sb1Bw1Ce1B1	186	25	808
		D34	Pw4Pr2Sb1Bw1Ce1B1	186	25	489
OG7	2	P56	Pw6Mh2Pr1Ms1	203	30	255
		J84	Pw6Mh2Pr1Ms1	203	30	87
OG8	2	R97	Pr5Pw2Bw1Po1Sw1	183	24	111
OG9	2	S123	Pw4Pr2Sb1Bw1Ce1B1	186	25	808
		D34	Pw4Pr2Sb1Bw1Ce1B1	186	25	489
MT1	2	P38	Pw3Pr3Pj1Sb1Po1Bw1	93	20	70
MT2	1	P74	Pw4Po2Pr2Sw1Bw1	79	23	36
MT3	2	E127	Pw4Pj2Pr1Sw1Po1Bw1	88	19	74
MT4	2	R162	Pw4Pr2Bw2Po1Sb1	83	19	59
MT5	2	V113	Pr4Pw3Po1Bw1Sw1	115	20	253
		V35	Pr4Pw3Po1Bw1Sw1	115	20	171
MT6	2	J52	Pw3Pr3Sb6Bw2Po1	78	19	52
MT7	4	R165	Pw7Bw2Po1	93	11	66
MT8	3	P66	Bw3Pw2Pr2Po2Ce1	101	15	206
MT9	2	E127	Pw4Pj2Pr1Sw1Po1Bw1	88	19	74

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[3] e.g.Pw7Bw2Po1= 70% White Pine, 20% White Birch, 10% Poplar

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APPENDIX A.1 - cont'd

[1] Site Class: A numerical expression of productivity of an area for a given species, determined from the appropriate figure in the normal yield table and expressed to the nearest full number. There are four site classes: X, 1, 2, 3 and 4 with X representing best site conditions, and '4' the poorest (Taken from Forest Resource Inventory maps).

Township Codes[2]
B- Briggs
D- Delhi
E- Eldrige
J- Joan
P- Phyllis
R- Riddell
S- Shelburne
St- Strathcona
V- Vogt

Species Codes[4]
Ab- Black Ash
B- Balsam Fir
Bw- White Birch
By- Yellow Birch
Ce- Cedar
Mh- Sugar Maple
Ms- Red Maple
Pj- Jack Pine
Po- Poplar
Pr- Red Pine
Pw- White Pine
Sb- Black Spruce
Sw- White Spruce

APPENDIX A.2- Number of study sites in each of 5 site classes (X, 1, 2, 3, 4). Site classes are determined from Forest Resource Inventory data, where 'X' is highest site quality and '4' is poorest.

		Old-growth	Mature	Managed
Site Class:	X	0	0	0
	1	1	1	0
	2	7	6	5
	3	2	1	5
	4	0	1	0
TOTAL		10	9	10

APPENDIX B- Results for normality and homoscedasticity tests for One-Way ANOVA's described in Table 1. Normality of residuals was tested using Lilliefor's test, and Bartlett's test was used for homoscedasticity of residuals.

Dep Var	Normality	Homoscedasticity
Blackburnian Warbler	p>0.146	p>0.699
Black-and-white Warbler	p>0.072	p>0.455
Black-throated Green Warbler	p>0.239	p>0.123
Solitary Vireo	p>0.072	p>0.398

Appendix C- Power analysis of One-Way ANOVA results described in Table 1.

Species	P	Power
Blackburnian Warbler	0.059	0.39
Black-and-white Warbler	0.613	0.05
Black-throated Green Warbler	0.070	0.36
Solitary Vireo	0.077	0.34

SUMMARY

Old-growth pine forests differed significantly from mature and managed forests in some characteristics of vegetation structure and diversity. These characteristics are: greater tree species diversity in the upper canopy, higher percent cover in the upper canopy, greater average number of vegetation layers, greater spatial variability in the number of layers, and greater canopy height. All these characteristics reflect the greater abundance of tall trees in old-growth stands. Other characteristics said to be "typical" of old-growth forests did not differ among forest types: all stands had large diameter trees, managed and old-growth stands had similar densities of large-sized snags.

No set of criteria has been identified which describe the prototypical old-growth forest ecosystem. Since forest development occurs along a continuum it is difficult to distinguish discrete classes of forests. The only criterion that all old-growth forests share is lack of catastrophic disturbance. This characteristic, along with the threatened status of this ecosystem, should provide sufficient justification for conservation of old-growth forests. Any other criteria will not represent the full range of old-growth ecosystems.

The abundances of all bird species studied were more strongly related to structural and floristic characteristics of habitat than to forest-type. Only Pine Warbler abundance differed significantly among forest-types, being more abundant in old-growth and mature than managed stands (i.e. pine vs. non-pine forests). The observed relationships between abundance patterns and habitat characteristics were similar to those reported elsewhere in other portions of the species' ranges. However, habitat characteristics were generally weak predictors of species' abundances with the exception of Pine Warbler. Pine Warbler abundance was strongly predicted by pine density, canopy height and number of species in the upper canopy. Loss of these habitat characteristics may strongly affect Pine Warbler abundance.