

DOE/OR/00033--T771

**EFFECTS OF LANDSCAPE COMPOSITION
ON EDGE-SENSITIVE SONGBIRDS
IN A FOREST-DOMINATED LANDSCAPE**

by

Brad McRae

A thesis submitted in partial fulfillment of
the requirements for the degree of

**MASTER OF SCIENCE
(LAND RESOURCES)**

~~DISTRIBUTION OF THIS DOCUMENT IS UNLIMITED~~

at the

MASTER

UNIVERSITY OF WISCONSIN-MADISON

1995

DISCLAIMER

Portions of this document may be illegible electronic image products. Images are produced from the best available original document.

Acknowledgements

First and foremost, I would like to thank the two people who helped to initiate and guide the development of this study. I am grateful to Virginia Dale, who took me on for a summer internship that led to this thesis at Oak Ridge National Laboratory, and to Tony Rinaldi, who provided the original inspiration to focus on songbirds, gave assistance and advice on many occasions throughout the project, and offered the use of the Nicolet National Forest Bird Survey data for my research.

I am very grateful also for the valuable advice and guidance given by my Madison committee members: Erhard Joeres, who has patiently watched me change directions many times over the years, Stan Temple, and Tom Lillesand. Thanks also to Tim Moermond for his feedback and participation as this project was wrapping up.

I am indebted to many Forest Service personnel for the time and assistance they provided during this study. Holly Kulinski, Dick Cutler, David Hoppe, and others were especially helpful in providing information and answering my many questions. Thanks to Tom Crow and John Probst at the North Central Forest Experiment Station for taking the time to brainstorm with a Madison graduate student who was eager to learn about ecology in northern Wisconsin.

Bob Howe provided excellent advice and guidance throughout this project, for which I owe many thanks. Monica Turner also provided inspiration, feedback, and numerous helpful suggestions, and generously offered the use of her office and workstation at Oak Ridge while she was in Yellowstone for the summer. Thanks also to Mark Meisenheimer, John Cary, and Eric Nordheim for their excellent statistical advice.

Thanks to Mike Mossman for offering the use of his cabin in Eagle River so that Lewis Jones and I didn't have to sleep in the rain while doing field work. Randy Wynne was very generous in sharing the use of the Silicon Graphics workstation, without which image processing would have been far more difficult.

I am grateful to the U.S. Department of Energy for funding the majority of this research. The research was performed under appointment to the U.S. Department of Energy, Graduate Fellowships for Global Change Program, administered by the Oak Ridge Institute for Science and Education.

I am especially thankful to my parents, Phyllis and O. Brent McRae, for not batting an eye when I gave up engineering for a less lucrative but more fulfilling career in ecology.

Finally, thanks to the IES staff, especially to Barbara Borns, for their assistance and support throughout my four years of graduate study. Thanks to my housemates at 1333 Mound Street for their wonderful patience and encouragement over the last two years.

Abstract

Thirty-eight mature upland forest stands in the Nicolet National Forest were selected to study relationships between abundances of edge-sensitive forest birds within the stands and patterning of vegetation types surrounding the stands. Ten indicator species were examined, and three years of point count data from the Nicolet National Forest Bird Survey formed the basis of the study.

Three separate habitat maps were created to quantify landscape structural characteristics in a geographic information system (GIS); the first was compiled from existing vegetation inventory maps maintained by the Nicolet National Forest, the second was based on a Landsat Thematic Mapper satellite image classification, and the third was based on a combination of the first two habitat maps.

Abundance of individuals in the indicator species group was related to statistical metrics of landscape pattern and proportions of habitat types surrounding the sites using multiple regression. Best subsets of variables to explain variation in total bird abundance were selected. Relationships between individual species abundances and landscape and site vegetation variables were also examined using univariate tests.

The combined habitat mapping method provided the best regression model of songbird abundance, and relationships given by this model were consistent across all species. Abundance of individuals in the indicator species group, taken in aggregate, was negatively correlated with proportions of upland open and regenerating forest, and positively correlated with mature upland mixed forest in the surrounding landscape.

This study suggests that forest fragmentation is negatively edge-sensitive songbird abundances in this region, and complements what is known about effects of forest fragmentation on birds in more agricultural and suburban landscapes. The study does not, however, provide evidence for or against reduced reproductive success due to habitat fragmentation. More research is needed to examine effects of fragmentation on nesting success and survivorship in this region.

Table of Contents

Acknowledgements	ii
Abstract	iii
Introduction	1
Methods	8
Site selection and bird census methods	8
Species selection	9
Habitat mapping	11
Site vegetation sampling	16
Landscape pattern analysis	18
Bird census data analysis	19
Multiple regression analysis	19
Single species tests	22
Results	23
Bird census data	23
Landscape variables	23
Multiple regression analysis	24
Single species test results	30
Discussion	34
Multiple regression analysis	35
Single species tests	39
Choice of indicator species	43
Habitat mapping scheme	44
Future prospects	45
Conservation implications	46
The need for studies of breeding success	48
Conclusions	49
References	52
Appendix 1	58

List of Tables

Table 1. Edge-sensitive indicator species list	10
Table 2. Aggregated Nicolet habitat types	11
Table 3. Landsat TM classification habitat types.	15
Table 4. Landscape variables considered in multiple regression analyses	21
Table 5. Additional variables considered in multiple regression analyses	21
Table 6. Species codes and numbers of sites used in univariate tests	23
Table 7. Multiple regression coefficients	27
Table 8. Univariate test results	31

List of Figures

Figure 1. Location of the Nicolet National Forest	4
Figure 2. Census site locations and federal ownership map	4
Figure 3. Illustration of habitat mapping schemes	17
Figure 4. Mature upland forest abundances within two buffer widths	25
Figure 5. Relationship between contagion and Shannon diversity	25
Figure 6. Relationship between mature upland forest and contagion	26
Figure 7. Indicator species group response to regenerating and open cover types	28
Figure 8. Indicator species group response to mature mixed forest	28
Figure 9. Indicator species group abundances within four Landtype Associations	29
Figure 10. Individual species responses to regenerating and upland open cover types	32
Figure 11. Individual species responses to mature mixed forest	32
Figure 12. Individual species responses to mature deciduous forest	33
Figure 13. Individual species responses to deciduous sapling densities	33

Introduction

Habitat fragmentation, a process in which once-continuous tracts of habitat are subdivided into discontinuous patches, has been recognized as one of the foremost current threats to biological diversity (Harris 1984, Wilcove et al. 1986, Noss and Harris 1986).

Habitat fragmentation is thought to threaten a wide range of organisms, of which neotropical migrant songbirds are a commonly cited example. These species breed in the United States and Canada during the spring and summer months, and winter as far away as Mexico, the Caribbean and Central and South America. Recent declines of many migrant songbird species have been attributed, in part, to fragmentation of the temperate forests in which they breed (Whitcomb et al. 1981, Ambuel and Temple 1983, Temple and Cary 1988, Terborgh 1989).

For neotropical migrant songbirds, fragmentation of breeding habitat involves more than a temporary reduction in habitat area. When forestland is converted to agricultural, residential, or other land uses, the remaining habitat is exposed to a suite of effects, whether the patches are isolated or internally fragmented (Temple and Wilcox 1986). Specifically, habitat fragmentation is thought to affect breeding songbirds by reducing patch sizes (Ambuel and Temple 1983, Lynch and Whigham 1984, Askins et al. 1987), isolating patches from the larger habitat matrix (Lynch and Whigham 1984, Askins et al. 1987, Robbins et al. 1989) and by creating edge effects; the latter may result in increased rates of nest predation (Gates and Gysel 1978, Wilcove 1985), increased brood parasitism (Brittingham and Temple 1983, Rich et al. 1994), altered competitive relationships (Butcher et al. 1981, Ambuel and Temple 1983), and other deleterious effects.

Much of what is known about the effects of habitat fragmentation on breeding songbirds is based on evidence from forest tracts embedded in predominantly agricultural or suburban landscapes (e.g., Whitcomb et al. 1981, Ambuel and Temple 1983, Lynch and Whigham 1984, Askins et al. 1987, Robbins et al. 1989 and others). Despite the apparent importance of habitat fragmentation to forest birds in other regions, little is known about the relationships between landscape structure and breeding bird distributions in extensively forested landscapes (Freemark 1989). Some researchers (e.g., Rudnick and Hunter 1993, Welsh and Healy 1993) have suggested that the results of studies in agricultural areas should not be directly applied to contiguously forested landscapes. Threats to songbirds (e.g., predation and brood parasitism) that have been identified in other areas may be less important in predominantly forested landscapes, where overall densities of predators and parasites may be low, and predators may be less concentrated along edges (Rudnick and Hunter 1993). Working in the midwestern United States, Robinson et al. (1995) compared nesting success in forests of nine different landscapes, ranging from predominantly agricultural to heavily forested. The study confirmed that nesting success is significantly higher in heavily forested landscapes; this result demonstrates differences in reproductive success *between* such landscapes and more agricultural landscapes, and complements studies that examine differences in nesting success rates within predominantly agricultural and suburban landscapes. Few studies, however, have examined the effects of fragmentation within extensively forested landscapes.

In predominantly forested landscapes, forest harvesting is a principal mechanism of habitat fragmentation, although intrinsic heterogeneity, natural disturbances, and societal

activities unrelated to forest management (e.g., summer home development, transmission lines, roads) may also fragment forest habitats (Stearns 1990). Most studies of forest harvesting impacts on birds in heavily forested landscapes have focused on the immediate site of disturbance (e.g., Conner and Adkisson 1975, Webb et al. 1977, Probst et al. 1992, Titterington et al. 1979, Niemi and Hanowski 1984, and others). These studies have demonstrated that bird species have differing tolerances for disturbance within forest stands, and have often documented recolonization of regenerating stands by forest birds in years following clearcutting or other major canopy disturbances. However, as in agricultural landscapes, forest fragmentation in these areas may involve secondary effects to adjacent lands. This study focused on whether such effects are impacting songbird abundances and distribution patterns in a heavily forested landscape.

The present study focused on the relationships between landscape pattern and edge-sensitive bird species in the Nicolet National Forest, a 655,000-acre area in northeastern Wisconsin (Figure 1). Besides being an example of a contiguously forested landscape, the Nicolet is of particular interest because it occupies a region of exceptionally high bird diversity. This region is the mixed hardwood-coniferous forest biome of the north-central and northeastern United States, which grades into boreal forest to the north and deciduous forest to the south (Curtis 1959, Temple 1979). Because species whose ranges lie principally to the north or south overlap in this transitional area, these mixed forests support an unusually high diversity of tree, shrub, and herb species (Mladenoff and Host 1994), and one of the most diverse avifaunas of any of the forests in North America (Temple et al. 1979). The region is also highly productive for many bird species relative to other parts of their ranges;

Figure 1. Location of the Nicolet National Forest.

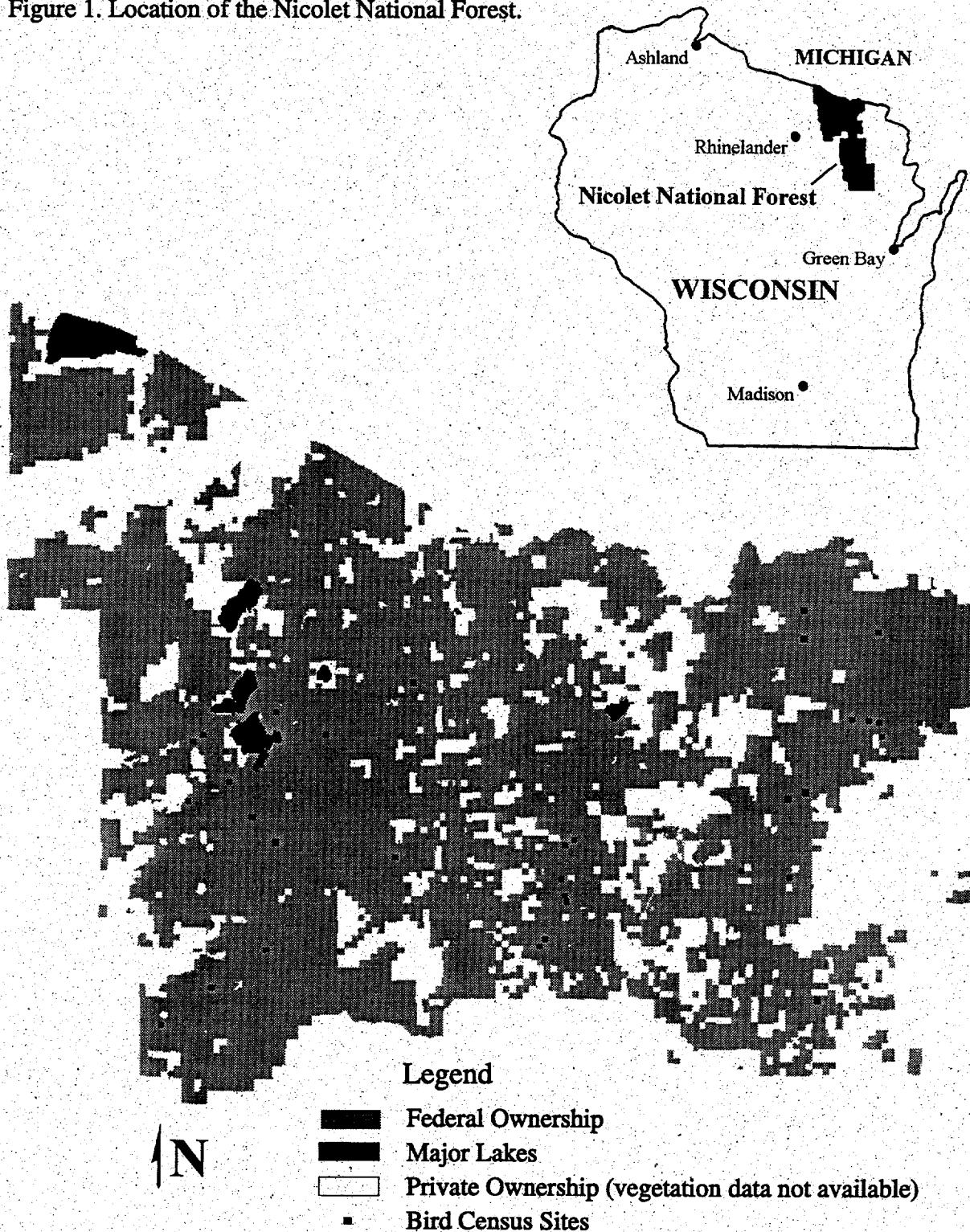


Figure 2. Locations of 38 bird census sites within the northern two districts of the Forest. Shading indicates federal ownerships, for which Nicolet vegetation data were available.

for many species a surplus of young produced in northern forests may be vital to the maintenance of underproducing populations in southern Wisconsin and elsewhere (Ambuel and Temple 1983, Howe et al. 1992, Robinson et al. 1995). This effect will be especially important for species with their geographic ranges centered in the region, such as the Ovenbird and the Blackburnian Warbler. These and several other species have been identified by Howe et al. (1992) as northern Wisconsin *source/core species*, or species that enjoy higher abundance or productivity in northern Wisconsin than in other regions.

The Nicolet National Forest occupies a highly diverse landscape, with glacial features (drumlins, moraines, pitted outwash plains) heavily influencing distributions of both overstory and ground-flora vegetation types (Mladenoff and Host 1994). The resulting landscape is a heterogeneous mosaic of forest, lake, bog, and marsh, dominated by upland and lowland coniferous, hardwood, and mixed forests.

Despite the heavily forested nature of much of the Nicolet, the landscape has undergone extreme changes in composition and spatial patterning of vegetation types during the past century. Prior to the establishment of the National Forests, much of northern Wisconsin's forests were logged, first selectively for white pine and hemlock, and later extensively for the remaining hardwoods (Curtis 1959, Alverson et al. 1988, Stearns 1990). The mixed hardwood-coniferous forest that predated these cuts has since been replaced in most areas by a younger, less diverse, second-growth forest. This forest has far lower abundances of once dominant or characteristic species like hemlock, yellow birch, and white pine, and correspondingly higher abundances of early-successional species like aspen and paper birch (Temple et al. 1979, Alverson et al. 1988, Stearns 1990, Mladenoff and Host

1994).

Contemporary timber harvest has replaced natural disturbance regimes as the principal source of young and early-successional forest patches in this region. Uneven-aged management in northern hardwoods stands, and even-aged management to maintain stands of early-successional species can be seen as modern analogues for natural treefall gaps and large-scale windthrow, respectively. However, the scale and frequency of these disturbances are very different from those of the pre-Columbian landscape; blowdowns tended to be much larger than modern clearcuts, but occurred at intervals of hundreds to thousands of years (Mladenoff and Host 1994, Curtis 1959). The superimposition of small harvest patches, high road densities, power corridors, summer home development, and other anthropogenic activities upon the forest has resulted in a landscape that is fragmented, but in a more complex and subtle way than in agricultural regions (Stearns 1990, Mladenoff and Host 1994). Mladenoff et al. (1992) found that human alteration of the landscape in this region resulted in reduced forest patch sizes, simplified patch shapes, greater numbers and types of successional patches, decreased late-successional and old-growth forest area, and creation of edge types uncharacteristic of old-growth forest conditions. These changes in landscape composition and pattern have raised concern over secondary effects such as increased abundances of edge-associated species, invasion of forest areas by exotic species, and the loss of forest interior habitat, in which many of the species of this biome evolved (Alverson et al. 1988, Crow et al. 1994).

The question of how fragmentation in the National Forests of northern Wisconsin affects forest species in general, and neotropical migrant songbirds in particular, remains

controversial. Based primarily on studies from other regions, Howe et al. (1992) proposed a set of 14 edge-sensitive indicator bird species for the Chequamegon and Nicolet National Forests. These species are thought to suffer from decreased fitness, productivity, and abundance in fragmented areas of northern Wisconsin as a result of increased pressures of predation, brood parasitism, and competition. Ten of these indicator species were included in this study; because these species were hypothesized *a priori* to be sensitive to habitat fragmentation, this group was considered ideal for statistical tests for effects of landscape pattern on species. The null hypothesis to be tested was that, in a particular forest stand, site vegetation characteristics determine the abundances of species within this group, and that the patterning of cover types in the surrounding landscape has no effect on the distribution or abundance of these species.

The alternative hypothesis was that landscape features, identifiable through mapping techniques used in this project, will affect species abundances within forest stands in the Nicolet National Forest. This hypothesis is based, as was the choice of indicator species, primarily on the results of studies conducted in other regions. Evidence from this region is mixed; a few studies elsewhere in the northern Lake states (e.g., Mason (unpublished data), and Dellasala and Rabe 1987) have shown that some forest birds avoid stands in close proximity to large openings like aspen clearcuts. Howe et al. (1993) documented higher abundances of American Crow (a potential nest predator) along roadside sites compared with forest interior sites of the Nicolet National Forest Bird Survey. However, Schneider (1992) found little evidence for effects of narrow logging roads on forest birds within the Nicolet National Forest. Clearly, there is much to be learned about the magnitude of fragmentation

effects and the scales at which they operate in this region. Different types of edges are likely to have different degrees of impact on forest birds (Howe et al. 1992).

Methods

This study examined abundances of ten edge-sensitive indicator species at 38 census sites in the northern half of the Nicolet National Forest (Eagle River and Florence Ranger Districts). Bird census data were acquired from the Nicolet National Forest Breeding Bird Survey, a cooperative effort of the Northeastern Wisconsin Chapter of the Audubon Society and the U.S. Forest Service. The 38 census sites were all located in mature upland forest stands, and represented a variety of stand characteristics and landscape contexts. The study compared abundance of individuals within the indicator species group across the sites, and tested for relationships between total bird abundance within, and landscape pattern surrounding, each site. The following section summarizes site selection and census methods used by the Nicolet National Forest Breeding Bird Survey; for a detailed description of these methods, see Howe et al. (1995).

Site selection and bird census methods

Sample points for the Breeding Bird Survey were chosen to represent general habitat types within the forest. Generally, points were located 100m or more within the target habitat type in order to reduce contact with adjacent habitat types or busy road corridors. A total of 160 habitat-based census points have been established for the northern half of the Nicolet in this manner. Censuses began in 1988 for the northern half of the Forest, and census data for

1990, 1992, and 1994 were utilized for this study.

Censuses were conducted on a single weekend in mid June between first light and 9:00 AM. Volunteers worked in teams, each led by an expert birder. Each team visited five to six of the habitat-based census points in a morning. At each census point all birds heard during a 10-minute period were recorded by species.

To reduce variation in local habitat features, I selected a subset of the 160 habitat-based census points based on the following criteria: only points occurring in mature upland forest stands that had been censused in each of the 1990, 1992, and 1994 census years were included; points occurring within pine plantations or stands with recent management activity were excluded; and points whose locations had been moved between census years were excluded. Following this procedure, 38 mature upland forest census points remained for inclusion in the study (Figure 2).

Species selection

Of the 14 edge-sensitive indicator species proposed by Howe et al. (1992) for the Nicolet and Chequamegon National Forests, eleven were recorded at the sites used for this study. Ten of these species occurred at four or more sites, and were included in statistical analyses (see Table 1). These species had three characteristics in common: they were all neotropical migrants, they were all forest species, and they had all been shown to be sensitive to habitat fragmentation in other regions.

Table 1. Edge-sensitive indicator species list from Howe et al. (1992). Numbers of sites with detections and individuals are summed across 38 sites over three years.

Species	Scientific Name	# Sites with Detections	# Individuals Detected
Red-eyed Vireo	<i>Vireo olivaceus</i>	38	197
Black-throated Green Warbler	<i>Dendroica virens</i>	35	152
Least Flycatcher	<i>Empidonax minimus</i>	25	94
Blackburnian Warbler	<i>Dendroica fusca</i>	21	59
Scarlet Tanager	<i>Piranga olivacea</i>	18	26
Black-throated Blue Warbler	<i>Dendroica caerulescens</i>	12	22
Solitary Vireo	<i>Vireo solitarius</i>	8	11
Black-and-white Warbler	<i>Mniotilla varia</i>	7	9
Wood Thrush	<i>Hylocichla mustelina</i>	6	8
Swainson's Thrush	<i>Catharus ustulatus</i>	4	4
Canada Warbler *	<i>Wilsonia canadensis</i>	1	7
Barred Owl *	<i>Strix varia</i>	0	0
Ruby-crowned Kinglet *	<i>Regulus calendula</i>	0	0
Spruce Grouse *	<i>Canachites canadensis</i>	0	0

* excluded due to low abundance or lack of detection

Habitat mapping

Two methods of vegetative cover mapping were used and compared for the landscape analysis portion of this study. The Nicolet National Forest maintains digitized vegetation maps (hereafter referred to as Nicolet stand data) in a geographic information system (GIS) for all federal ownerships within the Forest. This GIS contains information forest and non-forest cover types; for forest stands, the system provides information on forest type, size class, and stocking density. To facilitate landscape pattern analyses, the vegetation coverages were converted from their original MOSS GIS format to ARC/INFO (ESRI, 1994) format. They were then rasterized and converted to ERDAS (Erdas, 1994) format for processing, with a 25m x 25m pixel size. To simplify analyses, habitat types were aggregated into nine classes (Table 2).

Table 2. Nine aggregated habitat types and original Nicolet vegetation types.

Aggregated Habitat Type Code	Description	Original Nicolet Stand Data Code and Description
OPEN_NIC	Non-forested upland.	99: Non-forested Upland
REGEN_NIC	All upland forest types, seedling-sapling size classes.	All Upland Forest Types (1-5, 11, 17, 41-59, 81-93, 95)
UPDEC_NIC	Upland deciduous forest types, pole and sawtimber size classes.	53 Northern Pin Oak 54 White Oak 55 Northern Red Oak 59 Mixed Oaks 81 Sugar Maple-Beech-Yellow Birch 82 Sugar Maple-Basswood 84 Red Maple 85 Sugar Maple 86 Beech 89 Mixed Hardwoods 91 Quaking Aspen 92 Paper Birch 93 Bigtooth Aspen
UPCON_NIC	Upland coniferous forest types, pole and sawtimber size classes.	01 Jack Pine 02 Red Pine 03 White Pine 04 White Pine-Hemlock 05 Hemlock 17 Upland Black Spruce
UPMIX_NIC	Upland mixed forest types, pole and sawtimber size classes.	11 Balsam Fir-Aspen-Paper Birch 41 White Pine-Red Oak-White Ash 48 Jack Pine-Oak 49 Red Pine-Oak 87 Mixed N. Hardwoods, Hemlock 95 Aspen-White Spruce-Balsam Fir
LOFOR_NIC	Lowland forest types, pole and sawtimber size classes.	12 Lowland Black Spruce 14 Northern White Cedar 15 Tamarack 18 Mixed Swamp Conifer 19 Cedar-Aspen-Paper Birch 71 Black Ash-Am. Elm-Red Maple 76 Red Maple (wet site) 79 Mixed Lowland Hardwoods 94 Balsam Poplar
SCRUBCON_NIC	Lowland coniferous forest types, seedling-sapling size classes.	All Lowland Conifer Types (12, 14, 15, 18)
LO_OPEN_NIC	Lowland open (includes marsh, open bog, shrub swamp, sedge meadow).	97 Non-forested Lowland
WATER_NIC	Open water	LA: Open Water

The nine classes are an arbitrary grouping of the original forest types, but were designed to capture gross differences in habitat structure and composition. However, information (e.g., tree species) that may be important to songbirds may be lost in the aggregation. The conversion of the original vector-based GIS data to raster-based may also cause loss of information, as small polygons may not survive conversion to the 25m x 25m pixel size. Note that the original Nicolet classifications are based on the dominant forest type; upland deciduous classes may have significant coniferous components, and vice versa. Stands are classified as "mixed" by the Nicolet only if they fall into a typical mixed forest association, e.g., Balsam Fir-Aspen-Paper Birch or Jack Pine-Oak. Note also that although the aggregated lowland forest class contains both deciduous and coniferous forest types, coniferous forest dominates with 95% of the mapped area in this class.

In addition to census point locations, Figure 2 shows federally owned lands within the northern two districts of the Nicolet National Forest. The main drawback of using the Nicolet stand data was that they exist only for these federal ownerships. Private lands, or "inholdings", are not mapped, and the large proportion (approximately a third) of the Nicolet that is private results in maps with a considerable gaps in vegetation data. Also, major roads, power corridors, parking lots and other features do create openings in the forest canopy large enough to warrant consideration at this scale, yet these openings are often not captured by this dataset.

For these reasons, and to provide a second mapping method with which to compare results, I classified a 1991 Landsat Thematic Mapper satellite image for the same region, using the Nicolet stand data to generate training sets for the classification. The Landsat TM

image was acquired August 14, 1991; six spectral bands (three visible, three infrared) were available, with the original 30m resolution resampled to 25m. Unlike the Nicolet data, all vegetation cover is included regardless of ownership, all information in the scene is concurrent, and roads, power corridors, and other breaks in the canopy are included as open cover types if they are large enough to be mapped at 25m resolution. One major drawback to using Landsat TM data for habitat mapping is that there is very little ability to discern amongst different seral stages in upland forest types. Since the proportion of regenerating forest close to census points is of interest for this study, this shortcoming has important consequences that must be considered when comparing the utility of the Nicolet stand data with that of the Landsat TM classification.

The Nicolet stand data were used as reference data to generate training areas for image classification; training was performed on the Eagle River district, which occupies just over half of the study region. To generate training areas, the Nicolet stand data were compared with the Landsat TM scene, and polygons corresponding to homogeneous vegetation units in the Nicolet stand data were extracted from the Landsat TM scene for training. When extracting training areas, variable misregistration of up to 75m between the Landsat TM scene and Nicolet stand data became apparent. This misregistration resulted in nonhomogeneous training areas, because portions of vegetation units adjacent to the target units were often included in the areas.

To ensure that training areas would include only target vegetation types, polygons in the Nicolet stand data were "trimmed", eliminating pixels near edges of target vegetation units. To accomplish this, the ERDAS Scan/Boundary algorithm was used to identify all

pixels within 75m of any polygon boundary. Using the resulting "edge map" as a mask, a vegetation type map consisting of only core polygon areas was generated. Maps of each cover type were then generated from the resulting "core polygon map", and corresponding polygons on the Landsat scene were extracted for training. Visual inspection of the resulting training maps allowed for further refinement and verification of polygon homogeneity.

Information from aerial photographs, ground truth visits, and topographical maps was used to supplement and refine the training areas and the general classification process. Training areas for cover types that were under-represented in the Nicolet stand data (such as urban areas, roads, commercial cranberry bogs, and mixed hardwood-hemlock stands, which are typically classified with upland hardwoods under the Nicolet system) were added in this fashion.

Using bands 3, 4 and 5 of the Landsat TM image, a guided-clustering approach (Bauer et al. 1993; Fox and Mayer 1979) was used to generate spectral signatures from the training data. First, candidate signatures were generated for each class using the ERDAS Isodata algorithm. To ensure signature separability, the number of signatures generated for each cover type was chosen to maximize the Jeffries-Matusita (J-M) distance (see Swain and Davis 1978) between signatures. To choose the appropriate number of signatures for a given class, six signature sets, ranging from 15 to 20 signatures each, were generated using Isodata. The set with the highest minimum separability was chosen for further analysis, unless that set had a minimum J-M distance less than 1100. In this case, sets of 21 and progressively higher numbers of signatures were generated until the minimum separability exceeded 1100.

Guided clustering produced collections of candidate signatures for each cover type

which could subsequently be evaluated using preliminary classifications. Visual inspection of classified pixels and comparison with the forest stand data and aerial photographs allowed poor signature sets to be discarded. Separability between signature sets was assured again using the J-M distance as a comparison tool. Signatures between sets with low separability (again below 1100) were further evaluated using the ERDAS Quick Alarm utility or an actual classification, if necessary.

A limited amount of post-classification editing was performed to remove confusion among cover types that were systematically misclassified. Such confusion existed between jack pine plantations and lowland conifers, and between scrub conifer-leatherleaf bogs and some road corridors. In addition, a majority filter was applied to the scene to further improve classification accuracy and remove "noise" from the final habitat map. Final classes for the Landsat TM habitat map are shown in Table 3; Appendix 1 includes a discussion of accuracy assessment.

Table 3. Nine habitat types mapped using a 1991 Landsat TM image.

Habitat Type Code	Description
OPEN_TM	non-forest upland (recent clearcuts, roads, urban areas, etc.)
UPDEC_TM	upland deciduous forest (>80% deciduous)
UPCON_TM	upland conifer forest (>80% coniferous)
UPMIX_TM	upland mixed forest (20-80% deciduous)
LOFOR_TM	lowland forest
SCRUBCON_TM	scrub conifer-leatherleaf bog
LO_OPEN_TM	lowland open
WATER_TM	open water

Note that this classification scheme is similar, but not identical to the aggregated scheme for the Nicolet stand data. Of particular note are differences in ability to discern

regenerating from mature forest types and mixed from deciduous forest types. The Landsat classification does not differentiate regenerating from mature forest stands after canopy closure. This classification does, however, separate many mixed forest types (e.g., sugar maple/hemlock stands) from pure deciduous and coniferous stands, whereas much of the Nicolet stand data do not make this distinction.

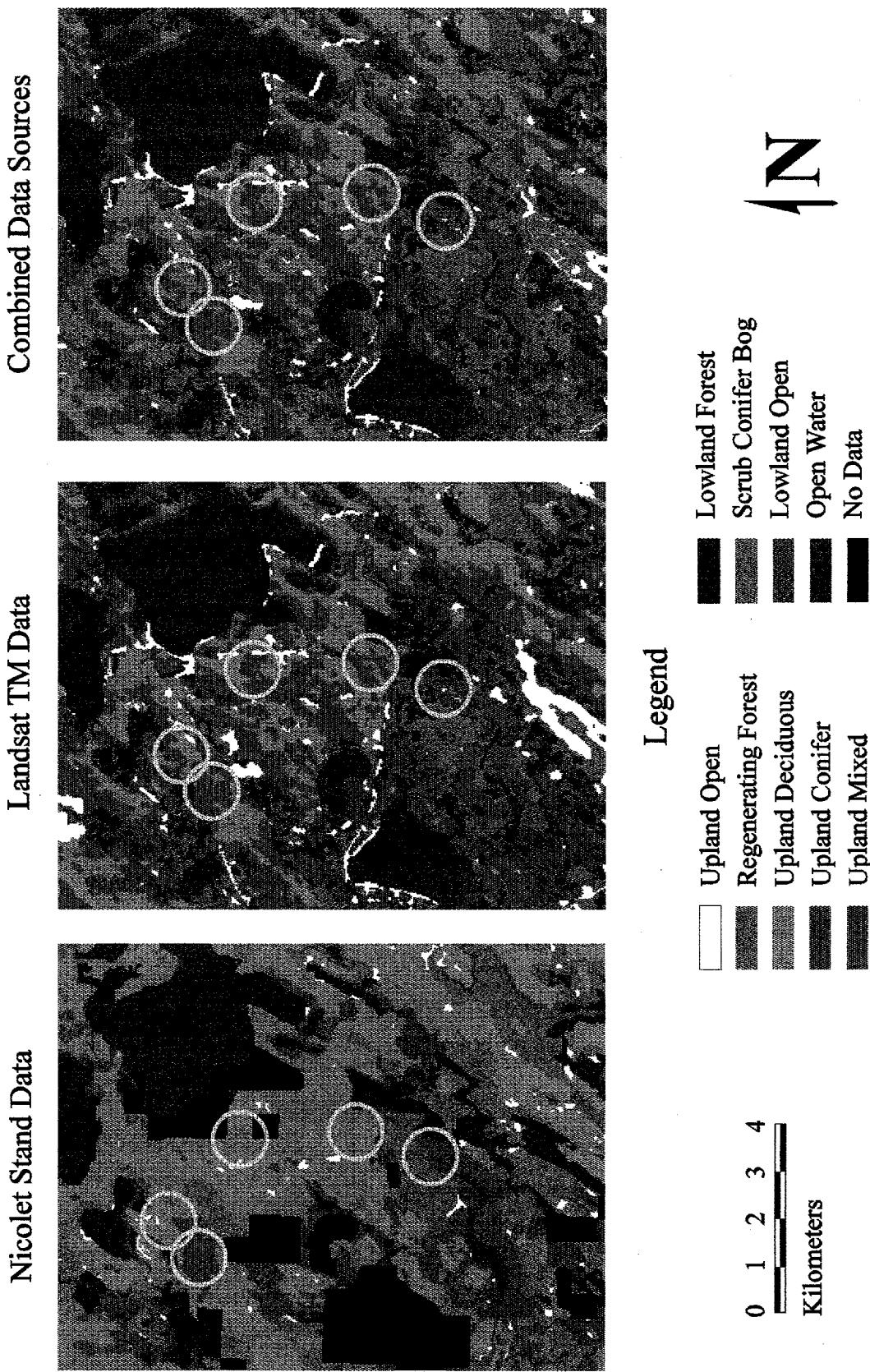
To take advantage of the strengths of each data source, a combination of the two was generated by adding the regenerating forest stands from the Nicolet stand data to the Landsat TM classification. This final habitat map provided the full coverage of the Landsat TM classification, included the mixed forest types of this classification, and included data on regenerating stands when available from the Nicolet dataset. Since remaining upland open cover types from the Landsat TM classification were often harvested areas on private lands, this type was aggregated with the regenerating stands from the Nicolet data to form a new OPEN/REGEN class. All other classes remained identical to those shown in Table 3; portions of the three habitat maps are shown in Figure 3.

Site vegetation sampling

For each bird census site, vegetation structure was sampled during the summer of 1994 to complement the landscape variables. The methods were chosen based on a synthesis of popular vegetation sampling techniques (e.g., James and Shugart 1970), and were intended to detect gross differences in vegetation structure between sites with a minimum of sampling time.

For each site, four 40m arm-length transects were run from the center stake in each of

Figure 3. Three habitat mapping schemes used for landscape variables. Region shown includes Butternut Lake (upper right), Sevenmile Lake (lower left), and an area burned in the Spring Lake fire of 1986 (horseshoe shape, bottom center). Circles represent 500m buffer widths surrounding five of the 38 census sites.



the four cardinal directions. Shrub and sapling stems less than 10cm dbh were counted in each of two height categories: 1.3m-3m and 3m-canopy; these were tallied in three life form categories: shrub, deciduous tree, and coniferous tree. The number of downed logs in two size classes (10-30cm and 30+cm dbh) were also tallied, and percent canopy closure, percent coniferous foliage in the canopy, and percent ground cover below 1.3m were estimated at five evenly-spaced points along each transect using an ocular tube (20 points per site). Transect measurements were averaged and summarized for each site. Finally, the distance to the nearest grassy opening (distance to edge) was recorded for each site.

Stand data on average tree diameter at breast height and Landtype Association (Jordan and Hoppe 1990) were obtained from Forest Service records to complement the vegetation data above. Landtype Associations are part of a developing hierarchical, ecological classification system for the Nicolet National Forest. They are based primarily on landforms, general soils, and general natural plant community information.

Landscape pattern analysis

All landscape variables included in subsequent statistical analyses were calculated using the FRAGSTATS spatial pattern analysis program for quantifying landscape structure, version 2.0 (McGarigal and Marks 1994). Variables quantifying aspects of landscape pattern were calculated first using the Landsat TM data for four circular buffer areas surrounding (and including) each sample stand. Buffer areas of 250m, 500m, 1km, and 2km radii were chosen *a priori* for these calculations (Figure 3 shows sample sites with 500m buffers indicated). These variables were again calculated using the Nicolet stand data and combined

data.

Variables calculated included percentage of all cover types identified by the Landsat TM classification and Nicolet GIS data within each respective buffer area. Also calculated for each buffer area were various pattern metrics including edge density (m/ha), a normalized contagion index (see O'Neill et al. 1988, Li and Reynolds 1993), Shannon diversity (Shannon and Weaver 1949), Shannon evenness, and an interspersion and juxtaposition index. For a complete description of metrics used and metric formulas, see McGarigal and Marks (1994).

Bird census data analysis

For each of the 38 sites considered in the study, three years of bird census data were summed for each of the ten edge-sensitive indicator species. Species abundances were summed over this period in order to reduce variability due to weather, annual fluctuations in abundances, observer differences, and random error in species detection. To construct a model of landscape effects on edge-sensitive species as a group, abundances for all ten indicator species were summed to create a single dependent variable for subsequent multiple regression analysis. The resulting values were natural log transformed to meet assumptions of the statistical tests used.

Multiple regression analysis

All subsequent data analyses were conducted using MINITAB for Windows, Release 9 (Minitab, 1993). Multiple regression analyses were first performed using stand and landscape variables from each of the four buffers (250m, 500m, 1km, 2km) for the Landsat

TM habitat map. Analyses were then repeated using the Nicolet stand data and the combined habitat map. Based on preliminary results, I chose to conduct these analyses using the 250m and 500m buffer widths only.

In order to produce an interpretable model of effects of landscape features on the indicator species, reduction in the number of independent variables was necessary. This reduction was particularly important given the inclusion of variables at multiple scales (e.g., mature upland forest at 250m, 500m, 1km and 2km buffers). Simple correlations between variables were examined, and in cases of high correlation ($r > 0.5$) the variable that was expected to yield the greatest explanatory power was retained.

In this manner, abundances of cover types within the various buffers were deemed preferable to statistical metrics of landscape pattern for inclusion in the final model. The latter metrics were generally highly correlated with each other and with abundances of individual cover types, yet appeared to possess lower predictive power than the cover type abundances themselves. Abundances of cover types (e.g., the amount of mature upland forest within 500m of census sites) were also considered to be more easily interpretable for management decisions than statistical metrics (e.g., contagion). In multivariate statistical tests, retaining highly intercorrelated variables yields final models whose predictive value for variables that do not follow the past pattern of multicollinearity are highly suspect (Morrison et al. 1992). This observation may be particularly meaningful in heterogeneous landscapes, since correlations between metrics and cover type abundances are likely to be very different in different regions. Due to differing habitat preferences between species, site vegetation variables were not considered in multiple regression analyses for the indicator species group.

In addition to landscape variables, distance to edge and Landtype Association were included in the regression analyses (see Tables 4 and 5).

Table 4. Landscape variables considered in multiple regression analyses. Variables represent percentages of respective cover types (see Tables 2 and 3 for descriptions of cover types).

Landsat TM Data (250m, 500m, 1km, 2km buffer widths)	Nicolet Stand Data (250m and 500m buffer widths)	Combined Data Sources (250m and 500m buffer widths)
%OPEN_TM	%OPEN_NIC	%OPEN/REGEN
%UPDEC_TM	%REGEN_NIC	%UPDEC
%UPCON_TM	%UPDEC_NIC	%UPCON
%UPMIX_TM	%UPCON_NIC	%UPMIX
%LOFOR_TM	%UPMIX_NIC	%LOFOR
%SCRUBCON_TM	%LOFOR_NIC	%SCRUBCON
%LO_OPEN_TM	%SCRUBCON_NIC	%LO_OPEN
%WATER_TM	%LO_OPEN_NIC	%WATER
	%WATER_NIC	

Table 5. Additional variables considered in multiple regression analyses. For Landtype Associations, numbers of sites within each LTA are also shown.

Variable	Description
DTE	Distance to nearest edge (m)
LTA (Categorical)	Landtype Association
LTA_7	Drumlinized uplands (n = 6)
LTA_A	Inter-drumlin pitted and unpitted outwash plain (n = 8)
LTA_B	Carpenter Lake outwash plain (n=1; omitted)
LTA_C	Popple River collapsed outwash plain (n = 15)
LTA_D	Hummocky outwash plain (n = 8)

Stepwise multiple regression analyses were used to eliminate variables with poor predictive power and produce final models for each of the three habitat maps. If two census sites were close enough to each other that their landscape maps overlapped by more than 20% at a given buffer width (e.g., 500m), one of the sites was randomly eliminated from any

analyses that included data at that scale. In this manner, analyses including data from the 500m buffer width excluded data from three sites (for a total of 35 sites).

Single species tests

Strong predictors of the edge-sensitive indicator species group were included in univariate tests of single species responses to site and landscape variables. For species with low abundances, presence and absence were used to distinguish “good” from “poor” sites; for more common species, sites with above-median abundances were used to distinguish good sites from poor. Sites with overlapping landscape data were treated in the same manner as described for multiple regression analyses; three sites were discarded for all tests within the 500m buffer. Two sample t-tests were used to test for differences in predictor variable values between good and poor sites for each species. Species codes for the ten indicator species are given in Table 6, along with median abundances and numbers of “good” and “poor” sites for each species. Numbers of “good” and “poor” sites are also given for tests of differences in landscape variables within the 500m buffer (three sites were discarded for this buffer due to overlapping landscape contexts).

Table 6. Species codes, median abundances, and numbers of “good” and “poor” sites used in univariate tests. Revised sample sizes for landscape variables within 500m buffer widths are also shown.

Species	Species Code	Median Abund.	#Good, Poor Sites (Total)	#Good, Poor Sites (500m)
Black-and-white Warbler	BAWW	0	7, 31	6, 29
Blackburnian Warbler	BLBW	1	11, 27	10, 25
Black-throated Blue Warbler	BTBW	0	13, 25	12, 23
Black-throated Green Warbler	BTNW	4	17, 21	16, 19
Least Flycatcher	LEFL	1	18, 20	16, 19
Red-eyed Vireo	REVI	5	15, 23	14, 21
Scarlet Tanager	SCTA	0	20, 18	17, 18
Solitary Vireo	SOVI	0	8, 30	5, 30
Swainson's Thrush	SWTH	0	4, 34	4, 31
Wood Thrush	WOTH	0	6, 32	5, 30

Results

Bird census data

For the ten edge-sensitive indicator species, a total of 582 individuals were recorded at the 38 sites during the 1990, 1992, and 1994 census years. Table 1 shows the number of individuals recorded for each species, and the number of sites at which each species was present during at least one census year.

Landscape variables

For the three habitat maps, high degrees of correlation were observed between landscape variables. Correlations between abundances of cover types at a given scale of measurement were variable, but often significant. For example, within the 250m buffer width, mature upland forest was highly correlated with non-forest upland ($r = -0.60$) for the

Landsat data. Correlations within a given cover class but between two buffer widths also presented problems; for example, mature forest within the 250m buffer width was highly correlated with mature forest within the 500m buffer width ($r = 0.90$) for the Landsat data (Figure 4). For the Nicolet stand data, these variables were correlated at $r = 0.825$.

High degrees of correlation were also observed between statistical metrics of landscape pattern (e.g., contagion and Shannon diversity, Figure 5) and between these metrics and cover type abundances (e.g., contagion and mature mixed forest, Figure 6). As noted previously, these metrics were dropped from further analysis due to their poor predictive power and high correlation with cover type abundances.

Multiple regression analysis

Three models of edge-sensitive indicator species abundances based on landscape variables were developed using stepwise multiple regression analysis. The first model is based on landscape variables retained from the Landsat TM data. The second model uses landscape variables calculated from the Nicolet stand data. A final model utilizes a combination of the Landsat and Nicolet data sources. The coefficients of these models are summarized in Table 7, and Figures 7 through 9 illustrate the relationships given in the combined model.

Figure 4. Relationship between mature upland forest within 250m buffer width and mature upland forest within 500m buffer width ($r = 0.90$). Thirty-eight sites are shown.

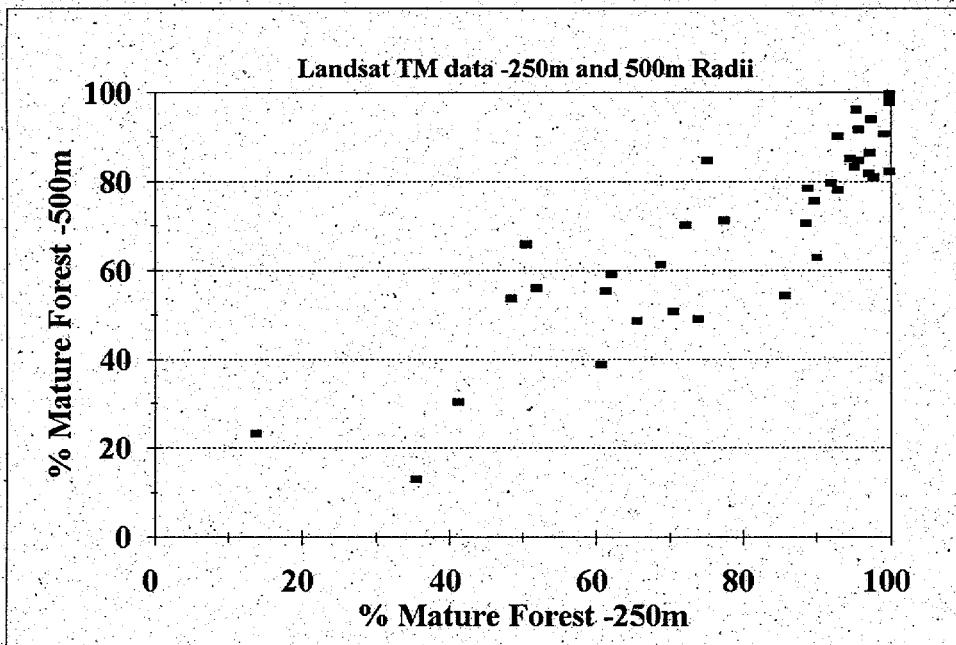


Figure 5. Relationship between contagion and Shannon diversity metrics within 500m buffer widths. Thirty-eight sites are shown.

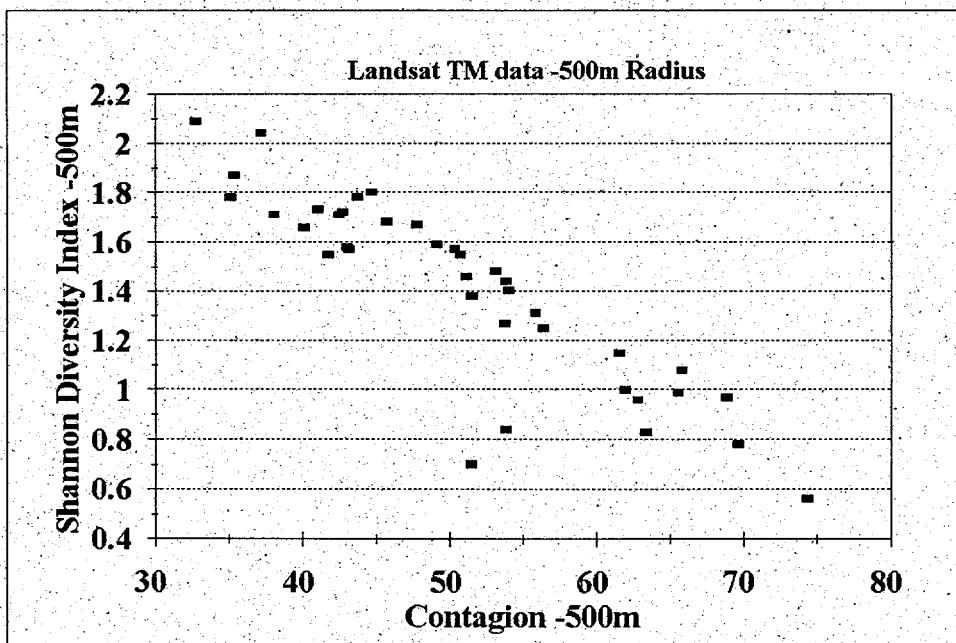


Figure 6. Relationship between mature upland forest and contagion within 500m buffer widths. Thirty-eight sites are shown.

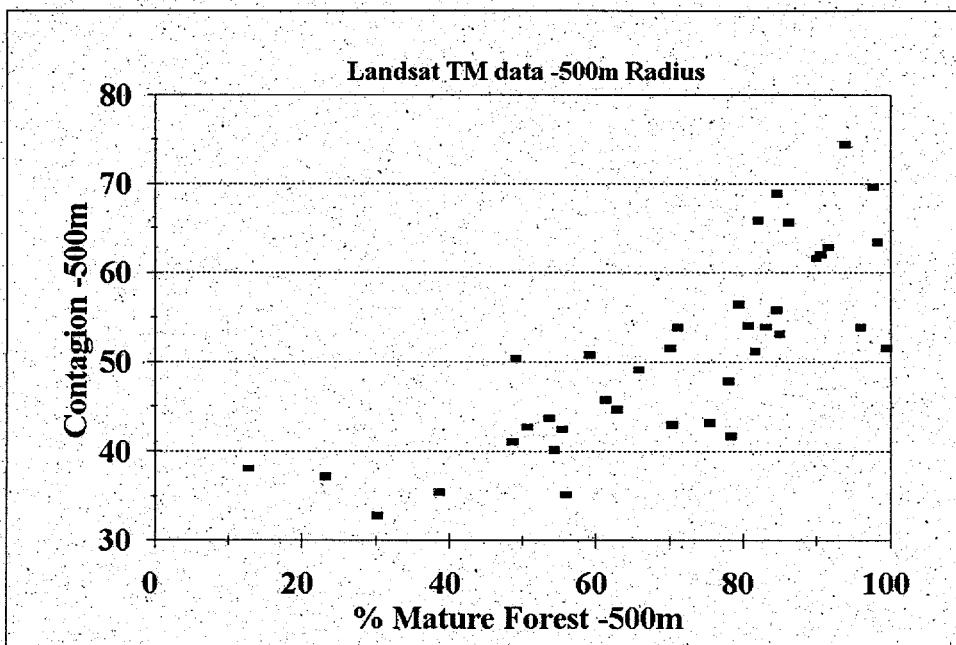


Table 7. Multiple regression coefficients for three models of effect of landscape variables on abundance of edge-sensitive indicator species. Abundance values are natural log transformed.

Landsat TM Model (n = 35, R² = 50.9%, R²adj = 46.1%)		
$\ln(\text{ABUND}) = 2.53 - 0.021(\%OPEN_TM) + 0.0078(\%UPMIX_TM) + 0.30(\text{LTA_D})$		
Variable	Description and buffer width	P-value
%OPEN_TM	% Upland open- 250m buffer	0.005
%UPMIX_TM	% Upland mixed forest- 500m buffer	0.028
LTA_D	LTA 'D': Hummocky outwash plain	0.030
Nicolet Stand Data Model (n = 38, R² = 53%, R²adj = 50.3%)		
$\ln(\text{ABUND}) = 2.79 - 0.021(\%REGEN_NIC) + 0.27(\text{LTA_D})$		
Variable	Description and buffer width	P-value
%REGEN_NIC	% Regenerating forest- 250m buffer	0.000
LTA_D	LTA 'D': Hummocky outwash plain	0.031
Combined Data Model (n = 35, R² = 60.0%, R²adj = 56.1%)		
$\ln(\text{ABUND}) = 2.61 - 0.014(\%OPEN/REGEN) + 0.0060(\%UPMIX) + 0.25(\text{LTA_D})$		
Variable	Description and buffer width	P-value
%REGEN/OPEN	% Regenerating and upland open- 250m buffer	0.001
%UPMIX	% Upland mixed forest- 500m buffer	0.061
LTA_D	LTA 'D': Hummocky outwash plain	0.046

Observed relationships between cover type abundances and indicator species group abundance were consistent between the Landsat and Nicolet stand data sources. Differences in the final regression models can be explained by differences in the classification schemes. Response to forest harvesting and other major disturbances to the forest canopy are best captured by the OPEN class in the TM classification scheme, and the REGEN class in the

Figure 7. Indicator species group response to regenerating and upland open cover types within 250m of census sites (from combined Landsat TM data and Nicolet stand data). Thirty-eight sites are shown.

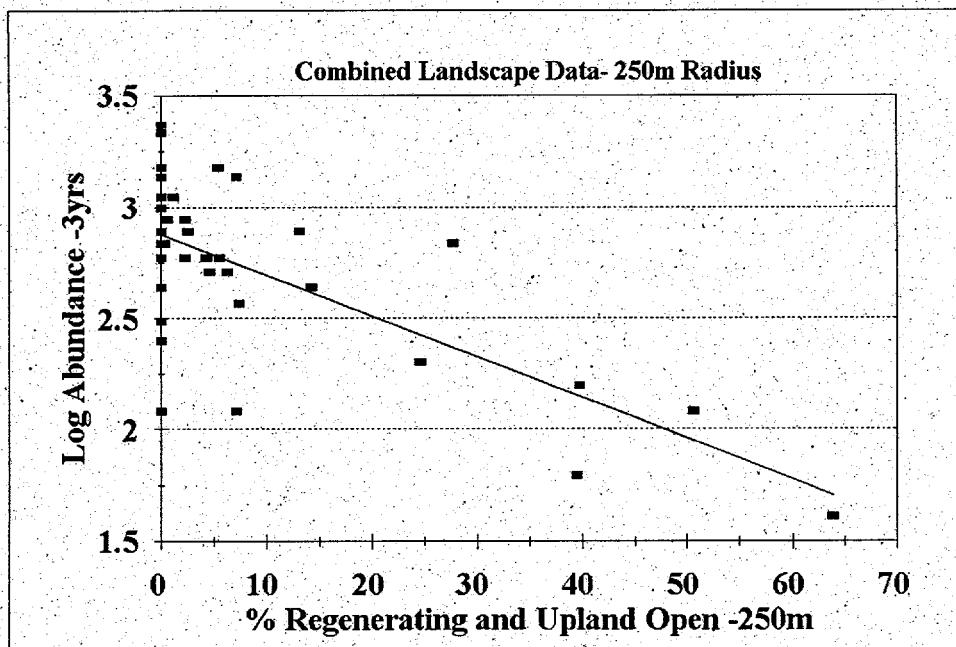


Figure 8. Indicator species group response to mature mixed forest within 500m of census sites (from combined Landsat TM data and Nicolet stand data). Thirty-eight sites are shown.

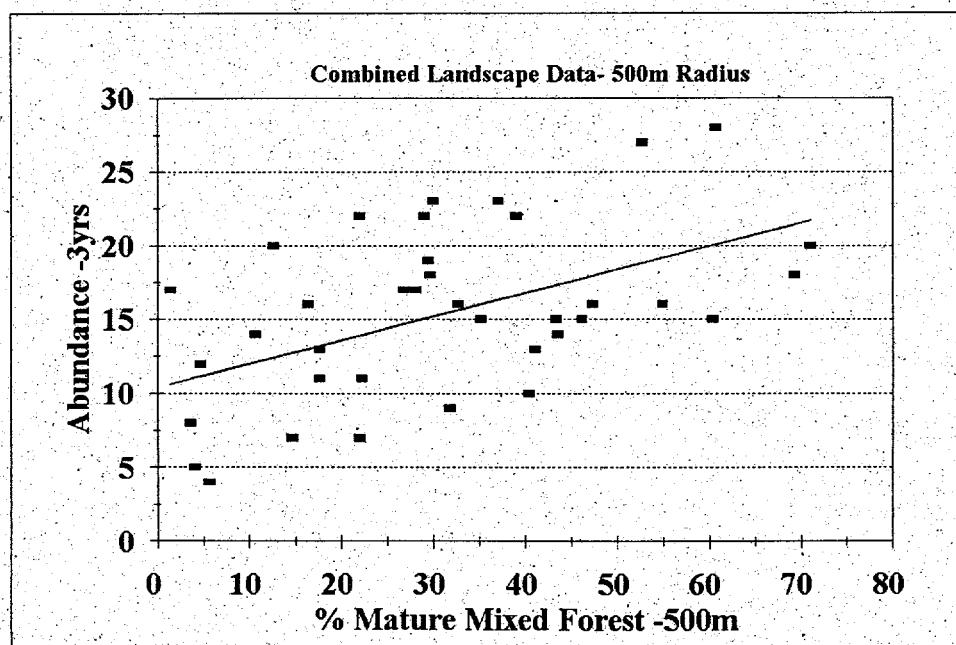
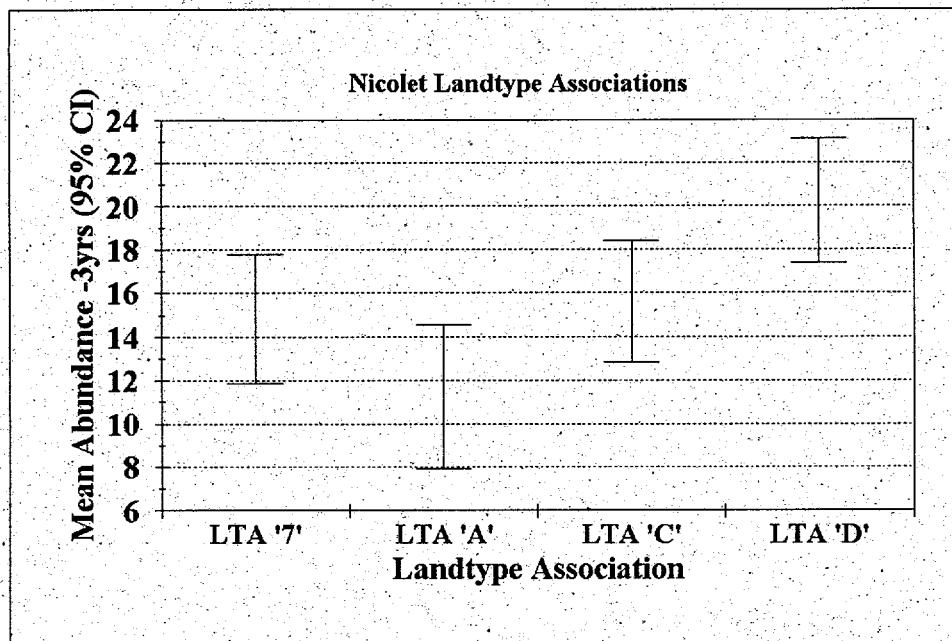


Figure 9. Indicator species group abundances within four Landtype Associations. Bars indicate 95% confidence intervals of mean abundances over 3 census years for each LTA.



Nicolet stand data.

Mature upland mixed forest (UPMIX) made a strong predictive contribution to the models based on the Landsat data, yet no forest types were included in the model based on the Nicolet stand data. Apparently, the UPMIX class in the Landsat TM classification captures habitat characteristics important to the species group, while these characteristics are not captured by any of the three mature upland forest classes compiled from the Nicolet classification scheme. As noted earlier, the Nicolet stand data and Landsat TM data differ in definitions used for mature upland mixed forest, and these differences are likely responsible for the model differences.

The inclusion of LTA_D as a significant predictor in the regression models indicates that this Landtype Association supports a higher density of individuals within the indicator species group than do each of the other LTA's considered. No significant differences among bird abundances between other LTA's were detected (Figure 9).

Single species test results

Univariate test results for species responses to site and landscape variables are summarized in Table 8. Figures 10 and 11 illustrate the responses to the landscape variables included in the combined regression model. For comparison, Figures 12 and 13 show individual species responses to variables not included in the regression models; Figure 12 shows individual species responses to mature upland deciduous forest within 250m of the census sites, and Figure 13 shows responses to densities of small deciduous saplings at the census sites.

Table 8. Univariate test results for selected landscape and site variables. P-values are shown for all variables for which $p < 0.25$. Landscape variables in bold were included in multiple regression models.

Landscape or Site Variable	Buffer width	Data Source	Species Code (see Table 6 for code definition)									
			BAWW	BLBW	BTBW	BTNW	LEFL	REVI	SCTA	SOVI	SWTH	WOTH
% Upland open	250m	Landsat	-0.11	+	-0.15	-0.055	-0.074	-0.23	-0.11	-0.23	-0.14	+
% Upland open	500m	Landsat	-	-	-	-0.70	-0.078	-0.24	-0.14	-	-	+
% Upland deciduous	250m	Landsat	-0.065	-0.050	+0.0074	+	+	+0.14	+	-	-0.24	-
% Upland deciduous	500m	Landsat	-0.021	-0.08	+0.035	+	+	+	+0.21	-	-	-
% Upland conifer	250m	Landsat	+	+	-0.01	-0.22	-0.006	-0.051	+	+	-0.20	-
% Upland conifer	500m	Landsat	+	-	-0.046	-0.17	-0.027	-	-	+	-	-
% Upland mixed	250m	Landsat	+	+	+	+	+0.058	+	+	+	+0.0009	+
% Upland mixed	500m	Landsat	+	+	+	+	+0.047	+0.093	+0.23	+	+0.07	+
% Regenerating forest	250m	Nicole	-0.19	-0.11	-	-0.024	-0.017	-	-0.14	-	-	-0.22
% Regenerating forest	500m	Nicole	-0.019	-0.015	+	-0.045	-0.021	-	-0.14	-	-	-
% Upland open/regen.	250m	Combined	-0.16	-	-	-0.018	-0.018	-	-0.12	-	-	-
% Upland mixed	500m	Combined	+	+	+	+	+0.020	+0.16	+	+	+0.11	+
% Canopy closure	--	Site	+	+0.25	+0.17	+0.017	+	+0.23	+	+	-	-
% Conifer in canopy	--	Site	+0.25	+0.048	-0.092	+0.19	-0.16	-	-0.10	-	+	-
% Ground cover	--	Site	-	-0.066	-	-0.0064	-	-0.25	-	-	-0.12	+
# Deciduous saplings <3m	--	Site	-0.13	-0.018	-0.094	-0.24	+0.12	+	-	+0.11	n.d.	+0.18
Distance to edge	--	Site	+	+	+	+	-	-	+0.11	n.d.	+0.18	-
Average tree diameter	--	Nic. site	+	+0.027	-	+0.023	+	-	+	+	+	+

Data sources: Landsat = Landsat TM classification; Nicole = Nicole stand data; Combined = Combined Landsat and Nicole stand data; Site = Sampled site vegetation data; Nic. site = Nicole site vegetation data. Responses: + = positive; - = negative; n.d. = no difference.

Figure 10. Average percent regenerating and upland open cover types within 250m of “good” and “poor” sites for individual species. Bars distinguish sites with above-median species abundances from sites with at- or below-median abundances. See Table 6 for species code definitions.

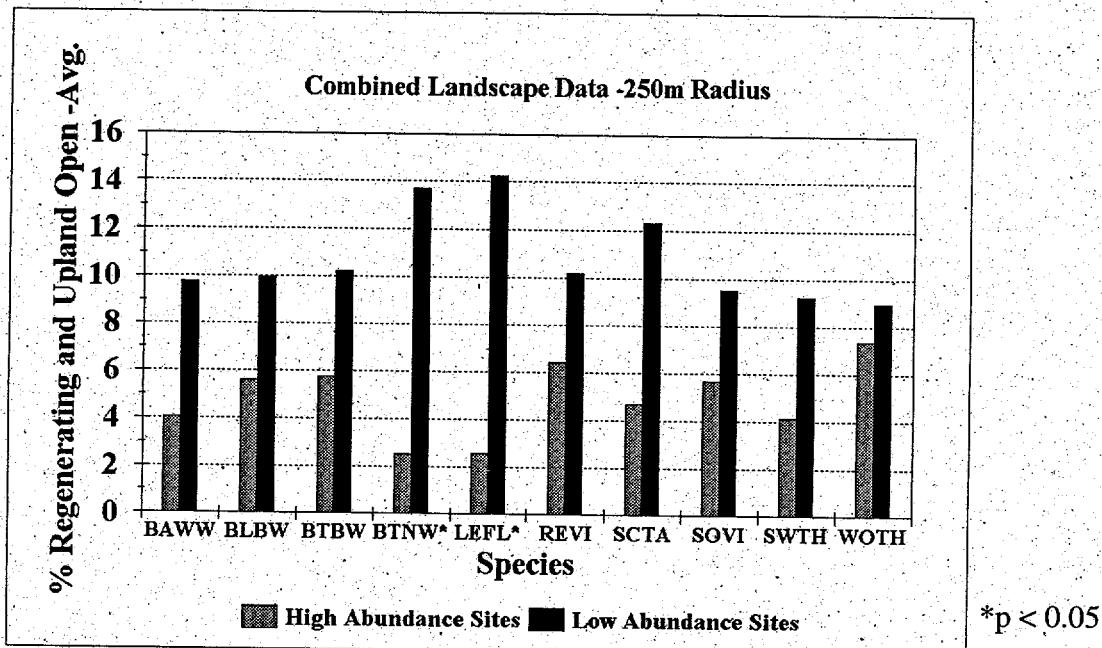


Figure 11. Average percent mature upland mixed forest within 500m of “good” and “poor” sites for individual species. Bars distinguish sites with above-median species abundances from sites with at- or below-median abundances. See Table 6 for species code definitions.

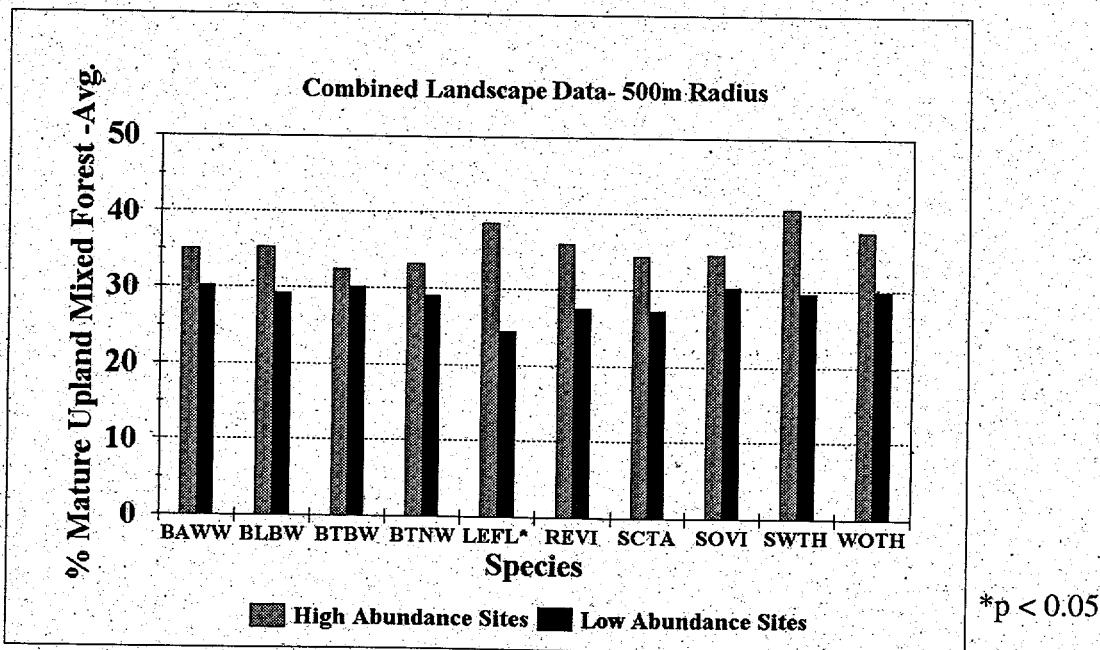


Figure 12. Average percent mature upland deciduous forest within 250m of “good” and “poor” sites. Bars distinguish sites with above-median species abundances from sites with at- or below-median abundances. Note the lack of consistent trends among species. See Table 6 for species code definitions.

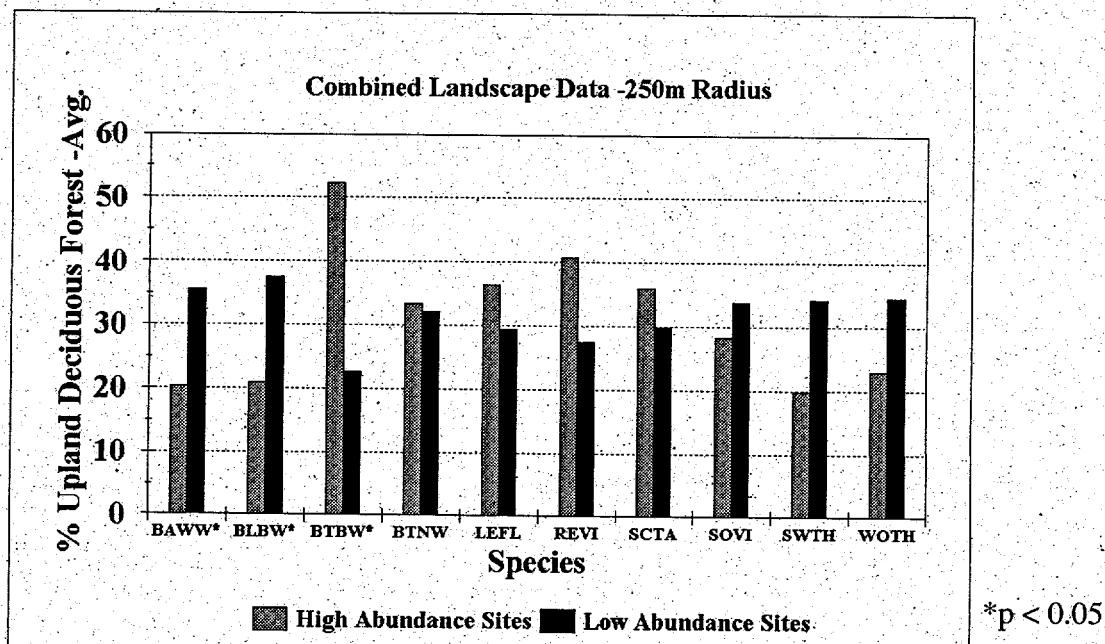
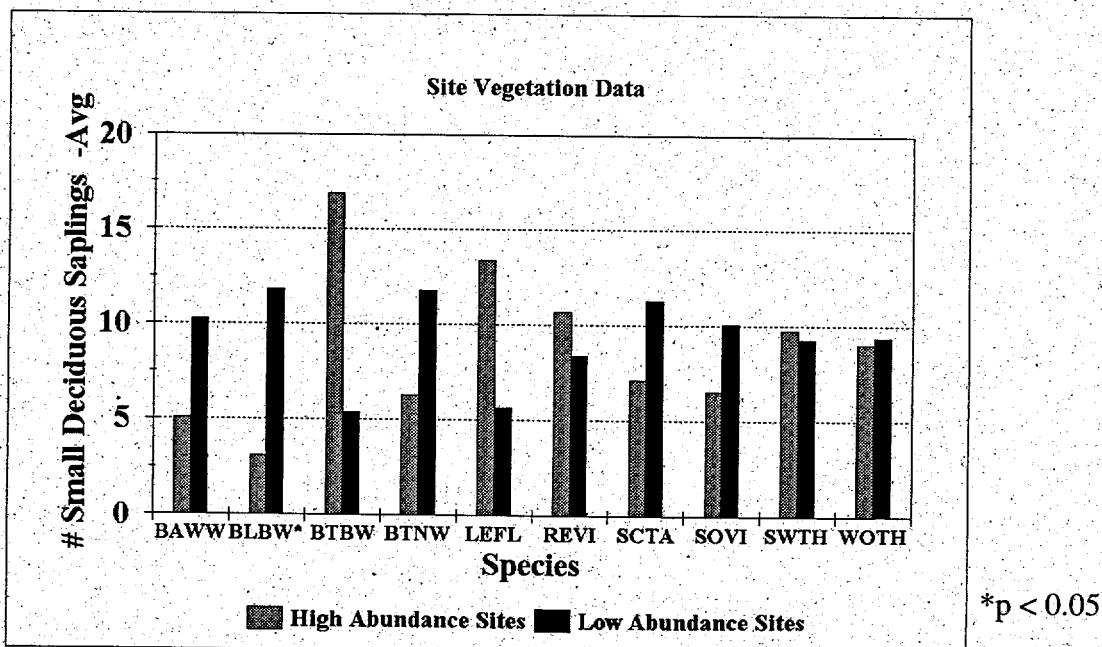


Figure 13. Average number deciduous saplings less than 3m tall from transects on “good” and “poor” sites. Bars distinguish sites with above-median species abundances from sites with at- or below-median abundances. Note the lack of consistent trends among species.



Discussion

Evidence of the relationship between landscape pattern and songbird abundances in the forests of the northern Lake states (Wisconsin, Michigan and Minnesota) is mixed. In the Nicolet National Forest, Schneider (1992) found little evidence for effects of narrow openings (mostly secondary road corridors) on the distributions of most songbird species considered. In the Chequamegon National Forest, D. Mason (unpublished data) found evidence for edge effects on birds in forest stands adjacent to aspen clearcuts. He documented that these effects lasted long after canopy closure, and were still evident after the canopy reached the height of the adjacent forest. In northern Michigan, Dellasala and Rabe (1987) found that Least Flycatcher aggregations nesting in large, continuous forests avoided large openings adjacent to the forests. In northwestern Wisconsin, Hawrot (1994) found that landscape features such as abundances of different vegetation types and edge types explained significant proportions of variation in abundances of ten bird species. In northeastern Minnesota, Pearson (1994) found significant correlations between landscape variables and four out of six bird species considered. The methods employed and questions pursued differ greatly among these studies, and generalizations of avian response to landscape pattern based solely on evidence from this region are not yet possible.

The present study differed from each of the above in that it involved a group of species chosen for a common hypothesized response to landscape pattern. This study indicates that landscape pattern, and particularly the abundances of certain land cover types, may play a strong role in determining abundances of individuals within this group of forest-dwelling songbirds. The strongest evidence for these effects was given by the multiple

regression analyses. Assuming that the indicator species respond to the same landscape characteristics at the similar scales, the greater power of multiple regression relative to two-sample t-tests in detecting responses to landscape pattern was to be expected. Although combining species abundances allowed greater power for detecting trends common to all species, this aggregation may have masked factors predictive for single species, but not shared among all species.

Multiple regression analysis

Three sources of landscape data were tested in the regression analyses: Landsat TM data, Nicolet stand data, and a combination of the two. The combined data source provided the best model of landscape features important to the edge-sensitive indicator species group. This result makes good sense, as the advantages of both data sources (i.e., the discrimination of mixed stands and inclusion of inholdings data from the Landsat TM data, and the discrimination of regenerating stands from the Nicolet stand data) were retained in the combined dataset. The implications of the regression results are that the indicator species group responds negatively to regenerating forest and open cover types within approximately 250m and positively to mature mixed forest within approximately 500m. Also, Landtype Association 'D' appears to support higher abundances within this species group relative to other Landtype Associations.

By far, the strongest predictors of indicator species group abundance in each of the models were abundances of regenerating and open cover types. These variables were most predictive for bird abundances within the 250m buffer, but were also predictive within the

500m buffer as well. The importance of these variables seems to extend beyond the simple fact that regenerating and open cover types are “nonhabitat” for these species; they remain important in regression models when forest abundance is taken into consideration, and are far more predictive of bird abundance than other “nonhabitat” types, such as non-forest lowland cover types. The combination of regenerating forest from the Nicolet stand data with upland open cover types from the Landsat TM classification provided the best predictor of bird abundance; this suggests that both recently harvested areas and permanent openings (e.g., power corridors, road right-of-ways, etc.) have an impact on the species considered.

Another consistent predictor for the indicator species group was abundance of mature mixed forest within the 500m buffer. The importance of this variable in predicting total indicator species group abundance is probably best explained by the fact that habitat requirements for all species considered overlap within mixed forest stands, while some species may avoid conifer or deciduous stands. Mixed forest stands likely represent habitat for all species considered, even though some species will respond only to the deciduous or coniferous component of these stands.

The different scales at which the two landscape variables were most predictive of bird abundance may indicate that different processes govern the relationship of these variables to the indicator species’ abundances. More research would be necessary to determine the mechanisms through which these characteristics influence species distribution patterns. It is interesting to note, however, that the scale at which regional forest abundance is most predictive (500m buffer width) contrasts with at least one study from more agricultural landscapes. For many species, including five of those considered in this study, Robbins et al.

(1989) found regional forest area within 2km to be more important than forest area at smaller (more local) extents. The difference in scale may be due to the fact that Robbins et al. conducted their study in a highly fragmented area, consisting of forest "islands"; isolation of forest blocks may have been very important to birds in this area, and may have been best measured by forest area within 2km. The Nicolet can be viewed more accurately as a contiguously forested landscape, with a certain degree of interspersion of forest with other habitat types. These other habitat types (bogs, lakes, clearcuts, wildlife openings, roads) may reduce regional forest area, but will not likely isolate forest stands from their neighbors. Mechanisms through which regional forest area might affect songbird abundances here remain unknown, but other studies in this region (e.g. Hawrot 1994, Pearson 1994) have shown the importance of forest abundance at similar scales.

The inclusion of Landtype Association 'D' as a significant predictor of indicator species group abundance indicates that the 'hummocky outwash plain' LTA supports a higher density of individuals within the indicator species group than do the other LTA's. Interpretation of this result should be made with caution; generally sites with a given LTA are in closer proximity to one another than sites with different LTA's. Differences in bird abundances due to factors such as harvest history, proximity to developed areas, relative abundances of certain cover types, and overall geographic variation in species distributions could easily be represented by LTA groupings. This variable will also be more closely linked with site vegetation than the landscape variables included in the models, and may be correlated with habitat characteristics important to a few of the species in the group.

Despite strong relationships detected using multiple regression analysis, caution must

be used when interpreting the results. Whenever possible, I used objective means to evaluate the predictive ability and theoretical basis for inclusion of each variable retained. The high levels of correlation between variables and between scales mean that variables included in the final model may be important in and of themselves or may simply be included as surrogates for other factors with which they are correlated.

Eliminating statistical metrics of landscape pattern and including only abundances of cover types in the final set of landscape variables was seen as a prudent move toward producing a model that was predictive, interpretable, and as free as possible of problems associated with correlated independent variables. Although they do show promise for describing landscape pattern in northern Wisconsin (see Mladenoff et al. 1992), the landscape metrics calculated for this study consistently showed lower potential to predict songbird abundances than the cover type abundances with which they were correlated. As noted previously, retaining the metrics would weaken the applicability of the models developed here to areas that do not follow the characteristic pattern of multicollinearity (Morrison et al. 1992).

Interpretation of the multiple regression results should also be made with caution when considering how *individual species* may respond to landscape pattern. The variables included were 'consensus' variables, or variables to which all or most species responded in the same direction. They are not necessarily the best predictors for each species. Prediction of how a given species will respond to changes in landscape pattern should include consideration of the single species test results, as well as additional evidence for that species, if available. Differences in site vegetation are likely to become far more important when

considering individual species.

Single species tests

Single species tests were conducted as a secondary method to determine relationships between species distributions and landscape pattern. The small sample size (38 sites) used in this study, combined with the relatively low statistical power of the univariate tests employed, limit the ability of the tests to make strong assertions about habitat preferences. Four species (Black-and-white Warbler, Solitary Vireo, Swainson's Thrush, Wood Thrush) were recorded at eight or fewer sites, further weakening the power of the univariate tests. For these reasons, the results of these tests will not be discussed in detail for all species. Still, some general conclusions can be reached from the results, and comparison with other studies may be more useful on a species-by-species basis.

Several of the statistically significant relationships agree with conventional knowledge of species habitat affinities. For example, the Blackburnian Warbler was found to respond positively to percentage of conifer in site overstories and to average diameter of trees within sample stands. This species responded positively to percent conifer within the stands and negatively to deciduous saplings < 3m tall. These results agree with several studies (e.g., Pearson 1994, Titterington et al. 1977 and others) that document this species' strong association with large conifers and open understories. Comparing effects of landscape variables, Pearson (1994) documented a positive relationship between this species' abundance and percentage of coniferous forest within 500m of census areas; this relationship was not found in the present study. However, the fact that "good" sites for this species had

significantly less deciduous forest within the landscape matrix than "poor" sites may demonstrate the same relationship. Blackburnian Warblers may be using mixed and coniferous forest, but avoiding areas with high regional abundances of deciduous forest due to lack of coniferous habitat or competition with deciduous-associated species. This species has been observed to use deciduous-dominated stands if some large conifers are present (D. Mason, unpublished data).

The positive response of the Black-throated Green Warbler to canopy closure agrees with the findings of Pearson (1994); however, the negative correlation with ground cover differs from the findings of Robbins et al. (1989). Positive relationships between mature upland conifer in the landscape (Pearson 1994) and tree diameter (Robbins et al. 1989, Titterington et al. 1979) were not observed in this study. Positive relationships with mature upland conifer in the surrounding landscape, and negative relationships with deciduous forest found by Pearson (1994) were also not observed. However, the affinity of this species for mixed forest may cloud relationships with regional abundances of coniferous or deciduous forest.

The Black-throated Green Warbler showed strong negative relationships with regional abundances of upland open and regenerating forest cover types. This species has been shown to be particularly sensitive to large-scale forest disturbance in other studies; Schneider (1992) found the Black-throated Green Warbler to be one of two species showing statistically significant avoidance of narrow logging roads in the Nicolet National Forest. Askins et al. (1987) found this species only in larger forests, and several studies (e.g., Webb et al. 1977, Titterington et al. 1979, Probst et al. 1992) have shown this species to be sensitive to forest

harvesting or have found the species only in mature stands.

The strong negative response of Least Flycatchers to upland open and regenerating cover types is also consistent with the findings of other studies. In large (> 100 ha) hardwood forests in Northern Michigan, Delasalla and Rabe (1987) found Least Flycatcher aggregations to be displaced away from forest openings at progressively larger distances as opening size increased. Webb et al. (1977) found this species to be negatively impacted by logging in a northern hardwood forest in the Adirondack Mountains of New York State. In the Nicolet National Forest, Schneider (1992) found no effect of narrow road openings on abundances of this species, but speculated that they may respond to larger openings such as those mapped in this study.

The Least Flycatcher showed at least moderately significant ($p < 0.10$) responses to ten out of twelve landscape variables tested. The tendency of this species to form aggregations (Bent 1942, Delasalla and Rabe 1987) may have contributed to the ability of the univariate tests used here to detect patterns in this species' distribution. Delasalla and Rabe (1987) suggest that aggregating Least Flycatchers may choose habitat that is removed from forest disturbances, with birds then selecting individual territories based on preferred site characteristics.

In contrast, no variables showed significance levels stronger than $p = 0.10$ for the Scarlet Tanager, despite a nearly ideal number of "good" and "poor" sites included in univariate tests for this species. Howe et al. (1993) found no statistically significant habitat preferences among major forest types for the Scarlet Tanager based on Nicolet National Forest Breeding Bird Survey data. These results and those from the present study indicate

that this species will be more of a habitat "generalist" than other species considered.

Furthermore, if the aggregational behavior of Least Flycatchers enhances the ability to detect habitat factors with which they are associated, then the more solitary, large-territorial behavior of the Scarlet Tanager may act to obscure these relationships. Note, however, that of the six factors for which $p < 0.15$, five are indicative of an avoidance of open or regenerating habitat types.

A number of more general observations can be made from the univariate test results. First, although more sophisticated statistical tests (e.g., multiple logistic regression, see Hosmer and Lemeshow (1989)) would be needed to evaluate the relative predictive contributions of each, site variables do not seem to yield greater predictive power for single species than do landscape variables. This result is surprising, since birds were expected to respond principally to local availability of resources, with landscape features acting secondarily to constrain, or modify the suitability of a given site for a species. The relatively weak significance of site variables for most species may be due in this case to the small area sampled for vegetation characteristics at each site, or omission of important variables in the sampling scheme. Also, site vegetation data were taken during the summer of 1994, and cannot be considered to be concurrent with any but the 1994 bird census data.

A second observation is that there is much greater consistency in the directions of responses within to landscape variables included in the multiple regression models (Figures 10 and 11) than to landscape variables not included in the models (e.g., upland deciduous forest within 250m buffer widths, Figure 12) or to site variables (e.g., deciduous sapling densities, Figure 13). For the combined landscape data, all species had positive relationships

with mature mixed forest within 500m of the census sites, and all had negative relationships with regenerating and upland open cover types within 250m. Other landscape and site variables tended not to show similar responses across all species. This result was to be expected because features which all species respond to in similar fashion are likely to be strongly correlated with summed abundances of all the species. Also, responses to site characteristics were expected to differ because the species group was chosen based on hypothesized response to landscape features (i.e., habitat fragmentation and edge), making no assumption about local habitat requirements or foraging strategies. Finally, the unanimity of responses of the species to regional abundance of regenerating and upland open cover types and mature mixed forest is further evidence that these features are important for the indicator species group as a whole.

Choice of indicator species

In recommending avian indicator species for the Chequamegon National Forest, Taylor (1990) states that an indicator of a particular habitat type should be so specifically associated with that habitat that a change in population will follow from, and unambiguously indicate, a change in the condition of the habitat. She notes, however, that several problems exist in the application of the indicator species concept, ranging from difficulties in monitoring indicator species to establishing a causal relationship between population trends and changing environmental conditions. Landres et al. (1988) recommend choosing several species to indicate particular environmental variables in order to avoid confounding effects of species-specific responses to changes in habitat. Trends among the chosen species could then

be confidently interpreted to reflect the desired habitat characteristics.

Although most tests for effects of landscape pattern on individual species did not produce statistically significant results, the consistency in direction of responses among the species to certain landscape variables, along with the results of multiple regression analyses, indicate a robustness in the choice of species by Howe et al. (1992). While local habitat requirements must be evaluated on a species-by-species basis, this group of indicator species, taken in aggregate, should provide a powerful monitoring tool for evaluating the effects of forest fragmentation and disturbance on edge-sensitive species in the region. The increased statistical power attributable to aggregating species abundances should also apply for studies of reproductive success, and is consistent with results from other studies. For example, Robinson et al. (1995) could not detect significant relationships between nest predation rates and percent forest cover for six out of nine species considered, yet found a strong overall effect across all nine species, with each contributing to the significance of the results.

Habitat mapping scheme

When evaluating habitat fragmentation, the scale at which organisms perceive the landscape must drive choices of scale and classification schemes for mapping habitat for those organisms (Pearson et al. 1995). Both the Nicolet stand data and Landsat TM classification apparently provide appropriate means of mapping landscape features important to the birds considered in this study. These results are encouraging, because the types of data used are readily available to land managers in the Nicolet National Forest and elsewhere in the northern Lake states. However, the scale of these data and the classification schemes

used are likely not ideal or comprehensive enough to capture all aspects of habitat fragmentation important to these species. Because forest types were aggregated into a simplified classification scheme, this study may not have made the most efficient use of the Nicolet stand data. By grouping forest classes, potentially useful information on tree species composition and community types may have been lost. Also, many sites were located in areas with notable levels of disturbance due to power corridors, recently harvested private lands, ski trails, forest roads, and other features that are not detected by either mapping scheme. Features such as unpaved roads as narrow as 8 meters have been shown to boost populations of nest predators and Brown-headed Cowbirds in New Jersey (Rich et al. 1994). Additional information about such features would likely improve models of avian response to fragmentation in this landscape as well. Still, the multiple regression results and the unanimity of species responses to regression variables from the combined mapping scheme argue strongly that this scheme captures landscape features important to edge-sensitive songbird species.

Future prospects

There is promise for incorporating results of studies like this one in other avian ecology research in this region. For example, a "moving window" approach could produce a map of landscape suitability for a species using hypothesized response to landscape pattern. Such a map could be used to stratify site selection for studies concerned with avian abundance and productivity, and predictions of bird abundances could be compared with observed densities. Stratification of sites by landscape characteristics would allow for

improved sampling design; for example, although this study found significant relationships between bird abundance and upland open and regenerating cover types, evidence of this relationship depended on a relatively small number of sites with high percentages of these cover types.

Simulations of population responses to different forest management scenarios could also make use of empirical relationships between species abundances and landscape pattern. Gustafson and Crow (1994) have constructed such a model to predict Brown-headed Cowbird parasitism levels under different forest management regimes. Similar models could be implemented to predict abundances of edge-sensitive songbird species in a changing landscape, and would have the potential to aid in forest planning efforts.

Conservation implications

Songbirds are conspicuous and charismatic features of the northern Wisconsin landscape; however, reasons to conserve these species extend beyond ethical or aesthetic arguments. More than ecological frills, there is growing evidence that the decline of insectivorous songbirds may threaten forest productivity. By eating insects that prey on the leaves of commercially important tree species, songbirds provide a first line of defense against the massive defoliation that these insects can cause. In a study of white oak (*Quercus alba*) productivity using nets to exclude insectivorous songbirds but not the insects they prey on, Marquis and Whelan (1994) found that trees with nets suffered twice as much leaf area loss as control plants. Holmes (1990) reviewed several studies on songbird insectivory and concluded that these birds play an important role in controlling populations of

leaf-eating insects. Severe insect infestations are not uncommon in the Nicolet, and recent outbreaks of spruce budworm, basswood thrips, and other insects have had major economic implications for timber harvesting in the Forest (R. Cutler, personal communication).

As the forests of northern Wisconsin recover from the massive clearcutting of the turn of the century, decisions of how to manage and restore the landscape will become more important. The National Forests may represent the only areas in the northern Lake states in which contiguous blocks of habitat can be maintained. Prudent forest management in the Nicolet National Forest would seek to reduce potential mechanisms through which forest harvest and conversion may impact breeding songbirds and other forest interior species. Simulations of harvesting effects on landscape pattern in the Pacific northwest (Franklin and Forman 1987) and in the midwest (Gustafson and Crow 1994) have shown that dispersing large numbers of small cutting units throughout the forest will create higher proportions of edge than using larger, more contiguous cutting units. If survivorship or breeding success is reduced in stands adjacent to openings or recently harvested areas, then concentrating harvests in some areas and removing other areas from intensive activities may be an effective conservation strategy.

This study also indicates that bird abundances within a given forest stand will be influenced by the composition of surrounding upland forest. Pearson (1994) found that several bird species were associated with conifers within census sites and with coniferous or mixed forest in the surrounding landscape. Although some species will respond to deciduous tree species and some to conifers, the positive association of all species abundances with mixed forest in the landscape suggests that the diversity of interior forest songbirds may be

favored by maintaining a conifer component within hardwood stands. Caution is in order when applying this conclusion to species outside of the indicator species group, however, and even to individual species within the group. More research is needed to understand the different competitive relationships that may occur in forest stands with different tree species composition.

This study did not compare impacts of different silvicultural systems (e.g., clearcutting, single tree selection, group selection, shelterwood methods) on songbirds; such comparisons would undoubtedly be useful for designing songbird management strategies on this landscape. Uneven-aged silvicultural systems, longer rotation periods, co-planting of conifers with naturally regenerating hardwood stands, snag and coarse woody debris retention, and attention to vertical and horizontal complexity when harvesting or performing intermediate cuts have been suggested to enhance habitat for non-game species in midwest forests (Tilghman and Evans 1986, Stearns 1990, Temple et al. 1979). The most prudent approach may mimic natural disturbance regimes or favor successional sequences that maintain and restore the heterogeneous hardwood-conifer character of the forest in which many species of this biome evolved. Special silvicultural treatments to increase abundances of formerly dominant or characteristic species (e.g., eastern hemlock, eastern white pine, yellow birch) will likely benefit many songbird species.

The need for studies of breeding success

In addition to limitations discussed previously, caution is necessary when interpreting differences in abundances of species as indicators of population health or habitat suitability

(Van Horne 1983, Taylor 1992). The regression analyses used here included only measures of abundance as dependent variables, without consideration of reproductive success. Studies of actual productivity of songbirds in the Nicolet would allow discrimination between the effects of wintering ground mortality and reduced breeding success. Furthermore, high abundance of a given species in a forest stand does not necessarily indicate high reproductive success for that species (Van Horne, 1983, Johnson and Temple 1986, Taylor 1992).

Monitoring reproductive success would give far greater insight into mechanisms affecting birds in this landscape. Based on breeding bird survey data, Brown-headed Cowbird abundances appear low in this landscape. However, nest parasitism by cowbirds has been documented for at least 14 species in the Nicolet (Howe et al. 1992), and Schneider (1992) reports observations of large numbers of cowbirds in the Diamond Roof area in May 1990 by UW-Green Bay researchers. He speculates that these individuals may have just been passing through the area, or that they may have been more detectable in May because of the lack of dense foliage or different behavior patterns at this time of year. More research is certainly needed to determine the extent and effects of cowbird parasitism and nest predation in this region.

Conclusions

This study has provided evidence that abundances of edge-sensitive forest birds within forest stands are affected by landscape composition in the Nicolet National Forest. Of particular importance were upland open and regenerating forest types, with which species abundances were negatively correlated. These results suggest that forest harvest and

conversion in the Nicolet National Forest have effects that extend beyond the immediate site of disturbance for these species.

Positive correlations between abundances of all species and mixed forest types within 500m of the census sites support hypotheses that bird species diversity is enhanced by the mixed nature of this region's forests. These relationships also suggest that elimination of a conifer component from northern hardwood stands in the Nicolet could have a negative impact on the bird communities within and adjacent to those stands. For individual species, abundances within any given forest stand are likely to be influenced by the amount of preferred forest habitat within the surrounding landscape. Mixed hardwood-conifer stands likely provide habitat for more species than do pure deciduous or coniferous stands; however, it is difficult to say whether regional bird diversity will be maximized by high abundances of mixed forest types or a mosaic of different forest types across the landscape (Temple et al. 1979).

The results of this study indicate appropriate choices of edge-sensitive indicator species by Howe et al. (1992) for this landscape. The scale and classification system used to map habitat surrounding census sites also seem appropriate, with a combination of existing vegetation survey and Landsat TM data sources providing the most powerful mapping scheme. The inclusion of finer-scaled data would undoubtedly improve this scheme, and the best habitat mapping method will most likely vary among species. Although some generalizations are possible and useful for this species group, individual species are likely to respond differently to forest fragmentation and to local and regional habitat characteristics.

This study was limited in that mechanisms through which forest disturbance affects

the species considered could not be evaluated. By choosing nesting and foraging areas away from major disruptions in the forest canopy, these species may be avoiding adverse effects associated with anthropogenic edge. Whether this choice actually equates with increased survivorship or productivity in this landscape is impossible to judge at this time. Nesting success, juvenile and adult survivorship, and long-term population trends need to be studied relative to forest fragmentation and landscape composition in northern Wisconsin. Fortunately, satellite imagery and existing vegetation survey data will likely be useful in evaluating landscape characteristics for such studies.

With its participation in the Partners in Flight program, the Nicolet National Forest has joined in a multinational effort to monitor and conserve neotropical migrant birds. The Nicolet has aggressively pursued monitoring and research activities in recent years, and is cooperating with a number of university researchers in the collection and use of bird census data. Ongoing and future studies will, hopefully, resolve remaining questions of how forest fragmentation and other human-induced modifications to the landscape affect songbird abundances and productivity in this region.

References

Alverson, W.S., D.M. Waller, and S.L. Solheim. 1988. Forests too deer: edge effects in northern Wisconsin. *Conservation Biology* 2(4):348-358.

Ambuel, B. and S.A. Temple. 1983. Area-dependent changes in the bird communities of southern Wisconsin forests. *Ecology* 64(5):1057-1068.

Askins, R.A., M.J. Philbrick, and D.S. Sugeno. 1987. Relationship between the regional abundance of forest and the composition of forest bird communities. *Biological Conservation* 39: 129-152.

Bauer, M.E., T.E. Burk, A.R. Ek, P.R. Coppin, S.D. Lime, T.A. Walsh, and D.K. Walters. 1994. Satellite inventory of Minnesota forest resources. *Photogrammetric Engineering and Remote Sensing* 60(3).

Bent, A.C. 1942. Life histories of north American flycatchers, larks, swallows, and their allies. U.S. National Museum Bulletin 179.

Brittingham, M.C. and Temple, S.A. 1983. Area dependent changes in the bird communities and vegetation of southern Wisconsin forests. *Ecology* 64:1057-1068.

Butcher, G.S., W.A. Niering, W.J. Barry, and R.H. Goodwin. 1981. Equilibrium biogeography and the size of nature preserves: an avian case study. *Oecologia* 49:29-37.

Conner, R.N. and C.S. Adkisson. 1975. Effects of clearcutting on the diversity of breeding birds. *Journal of Forestry* 73:781-785.

Crow, T.R., A. Haney, and D.M. Waller. 1994. Report on the Scientific Roundtable on Biological Diversity Convened by the Chequamegon and Nicolet National Forests. USDA Forest Service, General Technical Report NC-166.

Curtis, J.T. 1959. *The Vegetation of Wisconsin*. University of Wisconsin Press, Madison, Wisconsin.

Dellasala, D.A. and D.L. Rabe. 1987. Response of Least Flycatcher *Empidonax minimus* to forest disturbances. *Biological Conservation* 41:291-299.

Environmental Systems Research Institute, Inc. (ESRI). 1994. *ARC/INFO User's Manual*. Environmental Systems Research Institute, Inc., Redlands, California.

Erdas, Inc. 1994. *ERDAS Field Guide*. ERDAS, Inc., Atlanta, Georgia.

Fox, L. and K.E. Mayer. 1979. Using guided clustering techniques to analyze Landsat data for mapping forest land cover in northern California. Pages 364-367 in Proc. Symposium on Machine Processing of Remotely Sensed Data. Purdue University, W. Lafayette, Indiana.

Franklin, J.F. and R.T.T. Forman. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. *Landscape Ecology* 1(1):5-18.

Freemark, K.E. 1989. Landscape ecology of forest birds in the northeast. Pages 7-12 in R. DeGraaf and W. Healy, comps. *Is Forest Fragmentation a Management Issue in the Northeast?* USDA Forest Service, General Technical Report NE-140.

Gates, H.E. and L.W. Gysel. 1978. Avian nest dispersion and fledgling success in field-forest ecotones. *Ecology* 59(5):871-883.

Gustafson, E.J. and T.R. Crow. 1994. Modeling the effects of forest harvesting on landscape structure and the spatial distribution of cowbird parasitism. *Landscape Ecology* 9(4):237-248.

Harris, L.D. 1984. *The Fragmented Forest: Island Biogeographic Theory and the Preservation of Biotic Diversity*. University of Chicago Press, Chicago. 211 pages.

Hawrot, R.Y. 1994. Effects of Edge Type, Patch Shape, and Patch Size on Avian Communities in a Mixed Conifer-Northern Hardwood Forest. M.S. Thesis. University of Minnesota, Duluth, Minnesota.

Hoffman, R.M. 1989. Birds of Wisconsin northern mesic forests. *The Passenger Pigeon* 51(1):97-110.

Holmes, R.T. 1990. Ecological and evolutionary impacts of bird predation on forest insects: an overview. *Studies in Avian Biology* 13:6-13.

Hosmer, D.W. and S. Lemeshow. 1989. *Applied Logistic Regression*. John Wiley & Sons, New York, New York. 307 pages.

Howe, R.W., A.T. Wolf, and T. Rinaldi. 1995. Monitoring birds in a regional landscape: lessons from the Nicolet National Forest bird survey. Pages 88-95 in C.J. Ralph, J. Sauer, J. and S. Droege, eds. *Point Count Methods for Monitoring Population Trends in North American Birds*. USDA Forest Service, General Technical Report PSW-149.

Howe, R.W., S.A. Temple, and M.J. Mossman. 1992. Forest management and birds in northern Wisconsin. *The Passenger Pigeon* 54(4): 297-305.

James, F.C. and H.H. Shugart, Jr. 1970. A quantitative method of habitat description. *Audubon Field Notes* 24(6): 727-735.

Jordan, J.K. and D.J. Hoppe. 1990. Landtype Associations for the Nicolet National Forest. Draft manuscript.

Johnson, R.G. and S.A. Temple. 1986. Assessing habitat quality for birds nesting in fragmented tallgrass prairies. In Verner, J., M.L. Morrison, and C.J. Ralph, eds. *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates*. University of Wisconsin Press, Madison, Wisconsin.

Landres, P.B., J. Verner, and J.W. Thomas. 1988. Ecological uses of vertebrate indicator species: a critique. *Conservation Biology* 2(4):316-328.

Li, H. and J.F. Reynolds. 1993. A new contagion index to quantify spatial patterns of landscapes. *Landscape Ecology* 8:155-162.

Lillesand, T.M. and R.W. Kiefer. 1987. *Remote Sensing and Image Interpretation*. John Wiley & Sons, New York.

Lynch, J.F. and D.F. Whigham. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, U.S.A. *Biological Conservation* 28: 287-324.

Marquis, R.J. and Whelan, C.J. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology* 75(7):2007-2014.

McGarigal, K. and B.J. Marks. 1994. FRAGSTATS spatial pattern analysis program for quantifying landscape structure. User Documentation. Forest Science Department, Oregon State University, Corvallis, Oregon.

Minitab, Inc. 1993. *MINITAB Reference Manual, Release 9 for Windows*. Minitab, Inc., State College, Pennsylvania.

Mladenoff, D.J., M.A. White, J. Pastor, and T.R. Crow. 1992. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. *Ecological Applications* 3(2): 294-306.

Mladenoff, D.J., and G.E. Host. 1994. Ecological applications of remote sensing and GIS for ecosystem management in the northern Lake states. Pages 218-242 in Sample, V.A., ed. *Forest Ecosystem Management at the Landscape Level: the Role of Remote Sensing and GIS in Resource Management Planning, Analysis, and Decision Making*. Island Press, Washington, DC.

Morrison, M.L., B.G. Marcot and R.W. Mannan. 1992. *Wildlife Habitat Relationships*. University of Wisconsin Press, Madison.

Niemi, G.J., and J.M. Hanowski. 1984. Relationships of breeding birds to habitat

characteristics in logged areas. *Journal of Wildlife Management* 48(2):438-443.

Noss, R.F. and L.D. Harris. 1986. Nodes, networks, and MUMs: preserving diversity at all scales. *Environmental Management* 10:299-309.

O'Neill, R.V., Krummel, J.R., Gardner, R.H., Sugihara, G.I., Jackson, B., DeAngelis, D.L., Milne, B.T., Turner, M.G., Zygmunt, B., Christensen, S.W., Dale, V.H., and Graham, R.L. 1988. Indices of landscape pattern. *Landscape Ecology* 1:153-162.

Pearson, C. W. 1994. Effects of Habitat and Landscape Patterns on Avian Distribution and Abundance in Northeastern Minnesota. M.S. Thesis. University of Minnesota, Duluth, Minnesota.

Pearson, S.M., M.G. Turner, R.H. Gardner, and R.V. O'Neill. 1995. An organism-based perspective of habitat fragmentation. In R.C. Szaro, ed. *Biodiversity in Managed Landscapes: Theory and Practice*. Oxford University Press, Cambridge, U.K. *In press*.

Probst, J.R., D.S. Rakstad, and D.J. Rugg. 1992. Breeding bird communities in regenerating and mature broadleaf forests in the USA Lake states. *Forest Ecology and Management* 49:43-60.

Rich, A.C., D.S. Dobkin, and L.J. Niles. 1994. Defining forest fragmentation by corridor width: the influence of narrow forest-dividing corridors on forest-nesting birds in southern New Jersey. *Conservation Biology* 8(4):1109-1121.

Rudnick, T.C. and M.L. Hunter. 1993. Avian nest predation in clearcuts, forests, and edges in a forest-dominated landscape. *Journal of Wildlife Management* 57(2):358-364.

Robbins, C.S., D.K. Dawson and B.A. Dowell. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. *Wildlife Monographs* 103:1-34.

Robinson, S.K., F.R. Thompson, T.M. Donovan, D.R. Whitehead and J. Faaborg. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267(31):1987-1990.

Schneider, T.M. 1992. Effects of Logging Roads on Forest Birds in the Nicolet National Forest. M.S. Thesis. University of Wisconsin-Green Bay, Green Bay, Wisconsin.

Shannon, C. and W. Weaver. 1949. *The Mathematical Theory of Communication*. University of Illinois Press, Urbana, Illinois.

Stearns, F. 1990. Forest history and management in the northern midwest. Pages 107-122 in J.M. Sweeny, ed. *Management of Dynamic Ecosystems*. North Central Section, The Wildlife Society, West Lafayette, Indiana.

Swain, P.H. and S.M. Davis. 1978. *Remote Sensing: the Quantitative Approach*. McGraw Hill Book Company, New York.

Taylor, R.L. 1990. Avian indicators in the Chequamegon National Forest. *The Passenger Pigeon* 52(3):225-231.

Temple, S.A. 1988. When is bird habitat not habitat? *The Passenger Pigeon* 50:37-41.

Temple, S.A., and J.R. Cary. 1988. Modeling the dynamics of forest-interior bird populations in a fragmented landscape. *Conservation Biology* 2:341-347.

Temple, S.A. and B.A. Wilcox. 1986. Predicting effects of habitat patchiness and fragmentation. Pages 261-262 in J. Verner, M.L. Morrison and C.J. Ralph, eds. *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates*. University of Wisconsin Press, Madison, Wisconsin.

Temple, S.A., M.J. Mossman, and B. Ambuel. 1979. The ecology and management of avian communities in mixed hardwood-coniferous forests. Pages 132-153 in R.M. DeGraff and K.E. Evans, eds. *Management of North Central and North-east Forests for Non-game Birds*. USDA Forest Service, General Technical Report NC-51.

Terborgh, J. 1989. *Where Have all the Birds Gone?* Princeton University Press, Princeton, New Jersey.

Tilghman, N.G. and K.E. Evans. 1986. A framework for nongame management in midwestern forests. Pages 97-115 in J.D. Hale, L.D. Best, and R.L. Clawson, eds. *Proceedings of Management of Nongame Wildlife in the Midwest: A Developing Art*. North Central Section, Wildlife Society, West Lafayette, Indiana.

Titterington, R.W., H.S. Crawford, and B.N. Burgason. 1979. Songbird responses to commercial clear-cutting in Maine spruce-fir forests. *Journal of Wildlife Management* 43(3):602-609.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47(4):893-901.

Webb, D.L., D.F. Behrend and B. Saisorn. 1977. Effect of logging on songbird populations in a northern hardwood forest. *Wildlife Monographs* 55: 6-35.

Welsh, C.J.E. and W.M. Healy. 1993. Effect of even-aged timber management on bird species diversity and composition in northern hardwoods of New Hampshire. *Wildlife Society Bulletin* 21:143-154.

Whitcomb, R.F., C.S. Robbins, J.F. Lynch, B.L. Whitcomb, M.K. Klimkiewicz and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 125-205 in R.L. Burgess and D.M. Sharpe, eds. *Forest Island Dynamics in Man-dominated Landscapes*. Springer, New York.

Wilcove, D.S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:1211-1214.

APPENDIX 1: Landsat TM Classification Accuracy Assessment

This appendix details steps taken to ensure acceptable accuracy levels of the Landsat TM classification used in this study. As the study focused primarily on an ecological application of the image classification, rather than the actual classification process, time constraints have not allowed for traditional field reference data collection for accuracy assessment. However, the availability of an existing digital land cover dataset for reference, the Nicolet stand data, has allowed for a useful assessment of accuracy without the collection of manual ground truth data.

Accuracies were evaluated separately for the Eagle River Ranger District and for the Florence Ranger District. The two districts were evaluated separately because training areas were previously extracted entirely from the Eagle River Ranger District, which occupies just over half of the study region. All available reference data for this district were used to generate the training areas, precluding an independent evaluation of classification accuracy based on these data. Using training areas for accuracy assessment is problematic because the procedure will only determine the effectiveness of the classifier in reclassifying areas used to generate training statistics in the first place. This will typically result in an overly optimistic accuracy assessment. (Lillesand and Kiefer 1987). However, data from the Florence Ranger District data were not used for training, and could therefore provide an independent check of classification accuracy. Accuracy statistics, and absolute classification accuracy, can be expected to be somewhat lower for the Florence Ranger District because it is in a different area than the area used for training set acquisition. Statistics for this area will, however, be free of problems associated with using training areas for accuracy assessment, and will

provide a “worst case” assessment of overall classification accuracy.

Because the classification schemes of the reference data and the Landsat TM classification differ in some respects, traditional methods of accuracy assessment were somewhat modified. Specifically, the Nicolet stand data and Landsat TM classification schemes differ for the following classes: the regenerating forest class (REGEN) does not exist in the Landsat TM classification; mature upland mixed forest (UPMIX) in the Landsat TM scheme includes many forest types classified as deciduous (UPDEC) in the Nicolet stand data scheme; ground truth visits have shown that some features correctly classified as scrub conifer-leatherleaf bog (SCRUBCON) in the TM system are classified as lowland open (LO_OPEN) in the Nicolet system.

To evaluate accuracy given the above problems, two methods of computing accuracy statistics were employed for each district. The first assumes a one-to-one mapping of Nicolet and Landsat classes. This method most closely resembles traditional accuracy assessment techniques. The second method adjusts accuracy statistics by taking “acceptable reclassifications” into account and allowing for multiple correct classifications of reference pixels. In other words, a reference pixel is considered to be correctly classified if it is in the same class as the reference data, or within a set of classes that are deemed appropriate for reclassification. This may yield a more realistic evaluation because of differences in the two classification schemes; reclassification is actually desirable in certain circumstances, such as reclassification of deciduous forest types with a conifer admixture into the mixed forest class. Reclassifications judged to be acceptable for the purposes of accuracy assessment are shown in Table 1-1.

Table 1-1. Reclassifications of reference data considered acceptable for adjusted accuracy statistics.

Reference Class	Corresponding Landsat Class	Acceptable Reclassifications	Why Appropriate?
REGEN_NIC	NONE	OPEN_TM UPDEC_TM UPCON_TM UPMIX_TM	Recent clearcuts will appear as grassy openings. Older harvests will appear as mature forest in the Landsat classification.
UPDEC_NIC	UPDEC_TM	UPMIX_TM	Most upland mixed forest types are consistently classified as upland deciduous in reference data.
LO_OPEN_NIC	LO_OPEN_TM	SCRUBCON_TM	Ground truth visits have shown correctly classified scrub conifer-leatherleaf bogs to be classified as lowland open in reference data.

Although differences between the two classification schemes mean that the first, “unadjusted” accuracy assessment method will almost certainly yield overly pessimistic results, the second, “adjusted” method may be overly optimistic for two reasons. First, the larger number of “correct” classes for certain reference data types means that random “correct” classifications will be higher. Second, there is no method of determining whether a reclassification was appropriate for any given pixel; although we would expect a high number of pixels classified as upland deciduous forest to be reclassified into the mixed forest class, we cannot discern which reclassifications are correct and which are spurious.

Also important to note are reasons why the accuracy assessment statistics may be pessimistic, or lower than actual accuracy levels. The reference data are themselves

imperfect; errors and inconsistencies do exist in the Nicolet stand data, and certain features such as road corridors are not represented. Although training polygons were refined to eliminate areas that were not spectrally homogeneous (e.g., due to road corridors, misregistration), no such refinement was done for accuracy assessment polygons.

In summary, statistics based on a traditional one-to-one mapping of Nicolet and Landsat classification schemes can be expected to give a low estimate of classification accuracy, while the adjusted accuracy statistics will likely give a high estimate. Actual accuracy of the classification will likely be somewhere between the two estimates. Error matrices are given in Tables 1-2 through 1-5 for the two districts. Producer's and user's accuracies are given; producer's accuracies indicate the percentage of pixels in a given reference class that were correctly classified, while user's accuracies indicate the percentage of pixels within a given Landsat class that were correctly classified. Class averages measure the means of all within-class accuracies, while overall accuracies measure the total percentages of correctly classified pixels within the classification. Note that while most classes have large sample sizes of reference and classified pixels, accuracy statistics for classes with small sample sizes (i.e., OPEN for the Eagle River District) must be interpreted with caution.

Accuracies were highest for the Eagle River Ranger district, as expected, and adjusted accuracy statistics were substantially higher than unadjusted accuracy statistics. Overall accuracies ranged from 75.5% (unadjusted) to 90.8% (adjusted) for the Eagle River Ranger District, and 63.2% (unadjusted) to 90.3% (adjusted) for the Florence Ranger District.

High classification accuracies for upland deciduous (UPDEC) and water (WATER),

two of the most common cover types, contributed to high pooled accuracy statistics. Based on ground truth visits and aerial photo interpretation, confusion between certain lowland types (e.g., lowland open (LO_OPEN) and water (WATER)) seem to be due more to changing water levels and misregistration than to actual classification error. Problematic misclassifications included classification of upland conifer (UPCON) stands as lowland forest (LOFOR), classification of upland mixed forest (UPMIX) as upland conifer (UPCON) and lowland forest (LOFOR), classification of lowland forest (LOFOR) as lowland scrub conifer (SCRUBCON), and classification of lowland scrub conifer (SCRUBCON) as lowland forest (LOFOR). Confusion between these cover types is not surprising because they tend to be similar spectrally and structurally; however, improvement in discrimination between upland and lowland forest types would be especially desirable. Such improvement may be best accomplished by the use of vegetation indices that combine information from different bands.

This classification was judged to be adequate for the purposes of this study on several grounds. First, adjusted overall classification accuracies were high, exceeding 90%. Second, the Landsat TM classification appears to map upland open and mature upland deciduous, mixed, and coniferous forest types with high reliability; the discrimination of these types was particularly important for this study. Based on visual evaluation and comparison with topographic maps, low user's accuracies for the OPEN_TM cover type are likely due to openings in the forest canopy not mapped in the Nicolet stand data (e.g., due to road corridors and parking lots), rather than actual classification error.

For this study, confusion among lowland cover types has little effect on the statistical

analyses of bird distributions relative to habitat types. However, confusion between upland and lowland cover types remains problematic; pixels classified as upland conifer and upland mixed forest in the Nicolet system were often misclassified as lowland forest in the Landsat TM classification. Although there is room for improvement in classification accuracies for all cover types, elimination of confusion between upland and lowland forest would be of high priority for future studies of this type. Studies focusing on species associated with lowland habitats would require improvements in classification accuracies for lowland cover types as well.

Table 1-2. Error matrix showing numbers of pixels in reference and Landsat classes for the Eagle River Ranger District. Cells in bold indicate correct classifications and acceptable reclassifications used to calculate adjusted accuracy statistics.

Reference Class	Landsat Class								TOTAL
	UO	UD	UC	UM	LF	SC	LO	WA	
REGEN	425	512	396	1733	116	42	44	0	3268
OPEN	17	0	0	0	0	0	0	0	17
UPDEC	301	36992	274	11985	112	102	143	0	49909
UPCON	83	80	3052	617	995	166	16	34	5043
UPMIX	0	0	75	160	93	44	4	0	376
LOFOR	0	0	270	91	4765	1368	394	1	6889
SCRUBCON	27	0	115	2	1459	3986	319	207	6115
LO_OPEN	40	6	3	35	168	989	2299	266	3806
WATER	0	0	2	0	4	56	16	13398	13476
TOTAL	893	37590	4187	14623	7712	6753	3235	13906	88899

Landsat Class Codes: UO = OPEN_TM; UD = UPDEC_TM; UC = UPCON_TM; UM = UPMIX_TM; LF = LOFOR_TM; SC = SCRUBCON_TM; LO = LO_OPEN_TM; WA = WATER_TM. See Tables 2 and 3 for complete descriptions of Nicolet and Landsat classes.

Table 1-3. Error matrix showing producer's and user's accuracy rates for the Eagle River Ranger District. Percentages in bold were adjusted to take into account acceptable reclassifications. Note: Unadjusted accuracy statistics were calculated without inclusion of REGEN class, which is nonexistent in the Landsat TM classification scheme.

Reference or Landsat Class	# Ref. Pixels	# Classified Pixels	Producer's Accuracy	User's Accuracy	Producer's Acc. (adj.)	User's Acc. (adj.)
REGEN	3268	NA	NA	NA	93.8	NA
OPEN	17	893	100	3.6	100	49.5
UPDEC	49909	37590	74.1	99.8	98.1	99.8
UPCON	5043	4187	60.5	80.5	60.5	82.4
UPMIX	376	14623	42.6	1.2	42.6	94.9
LOFOR	6889	7712	69.2	62.7	69.2	61.8
SCRUBCON	6115	6753	65.2	5940	65.2	73.7
LO_OPEN	3806	3235	60.4	72.0	86.4	71.1
WATER	13476	13906	99.4	96.3	99.4	96.3

Overall Accuracy = 75.5%

Producer's Class Average = 71.4%

User's Class Average = 59.4%

Overall Accuracy (adj.) = 90.8%

Producer's Class Average (adj.) = 79.5%

User's Class Average (adj.) = 78.7%

Table 1-4. Error matrix showing numbers of pixels in reference and Landsat classes for the Florence Ranger District. Cells in bold indicate correct classifications and acceptable reclassifications used to calculate adjusted accuracy statistics.

Reference Class	Landsat Class								TOTAL
	UO	UD	UC	UM	LF	SC	LO	WA	
REGEN	742	856	1196	7260	636	260	295	0	11245
OPEN	195	0	0	1	2	0	0	0	198
UPDEC	249	32025	421	18618	362	98	126	0	51899
UPCON	79	17	4935	331	568	94	0	0	6024
UPMIX	24	47	164	231	134	8	0	0	608
LOFOR	22	8	822	146	5146	1354	447	82	8027
SCRUBCO	1	0	59	3	453	703	16	0	1235
N	30	3	13	80	179	525	952	283	2065
LO_OPEN	0	0	0	0	0	0	0	317	317
WATER									
TOTAL	1342	32956	7610	26670	7480	3042	1836	682	81618

Landsat Class Codes: UO = OPEN_TM; UD = UPDEC_TM; UC = UPCON_TM; UM = UPMIX_TM; LF = LOFOR_TM; SC = SCRUBCON_TM; LO = LO_OPEN_TM; WA = WATER_TM. See Tables 2 and 3 for complete descriptions of Nicolet and Landsat classes.

Table 1-5. Error matrix showing producer's and user's accuracy rates for the Florence Ranger District. Percentages in bold were adjusted to take into account acceptable reclassifications.

Note: Unadjusted accuracy statistics were calculated without inclusion of REGEN class, which is nonexistent in the Landsat TM classification scheme.

Reference or Landsat Class	# Ref. Pixels	# Classified Pixels	Producer's Accuracy	User's Accuracy	Producer's Acc. (adj.)	User's Acc. (adj.)
REGEN	11245	NA	NA	NA	89.4	NA
OPEN	198	1342	98.5	32.5	98.5	69.8
UPDEC	51899	32946	61.7	99.8	97.6	99.8
UPCON	6024	7610	81.9	76.9	81.9	80.6
UPMIX	608	26670	38	1.2	38	97.9
LOFOR	8027	7480	64.1	75.2	64.1	68.8
SCRUBCON	1235	3042	56.9	25.3	56.9	40.4
LO_OPEN	2065	1836	46.1	61.8	71.5	51.9
WATER	317	682	100	46.5	100	46.5

Overall Accuracy = 63.2%

Overall Accuracy (adj.) = 90.3%

Producer's Class Average = 68.4%

Producer's Class Average (adj.) = 77.5%

User's Class Average = 52.4%

User's Class Average (adj.) = 69.5%