

**INFLUENCE OF SCALE (GRAIN AND EXTENT)
ON EXPLAINING BIRD DISTRIBUTION
IN HUMAN-DOMINATED LANDSCAPES
OF EASTERN ONTARIO, CANADA**

By

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ABSTRACT

The appropriate spatial scale for ecological investigation is crucial because patterns and controlling processes may operate at different scales. Using remotely sensed data, I examined the effect of changing grain (4 m - 1 km) and extent (90 m -10 km) of 5 variables on explaining the variation in bird community composition in Eastern Ontario. Variation partitioning using canonical correspondence analysis revealed subtle differences between the amount of variation uniquely explained by the variable grains and extents examined. Forest amount at the finest scale accounted for nearly a third (29%) of the total variation (48%) accounted for in the bird data, but all variable grains and extents were significant. While sampling across a broader environmental gradient will help clarify the roles of variable grain and extent, these results reinforce the importance of fine-scale habitat composition and incorporating variables measured at a range of grains and extents in bird community modelling.

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1 INTRODUCTION

It is well established that ecological patterns and the processes that determine them are scale-dependent, in that the observed pattern and variability change with the scale of description (Wiens, 1989a; Levin, 1992; e.g. Sherry and Holmes, 1988; Rahbek and Graves, 2001; Luoto et al., 2007). Spatial and temporal scale dependencies are the indirect result of heterogeneity in the environment caused by abiotic factors such as climate, disturbance, and human land-use, as well as biotic interactions (Turner, 2005). Environmental heterogeneity creates variability in the distribution of resources, competitors and predators, since individuals perceive and respond to environmental heterogeneity at a range of scales based on individual species' life history adaptations such as dispersal and dormancy (Levin, 1992). Therefore, the choice of scale for ecological analysis cannot be assumed or imposed arbitrarily, *a priori*, but must instead be extracted from an analysis of observed data (King, 2005).

The degree that measurements made on a system at a given scale reveal something about ecological mechanisms is a function of system openness, or the extent to which patterns at one scale are influenced by those at broader scales (Wiens, 1989a). Ecosystem processes may be organized into discrete, hierarchically structured scales of interaction that impose discrete patterns on the landscape (Allen and Starr, 1982; O'Neill et al., 1986), and may explain how broad-scale processes constrain finer-scale phenomena. Physical determinants of biological phenomena are most likely to be evident at coarse scales. For example, at regional levels, energy has been strongly linked to patterns of vegetation and animal species richness (Currie, 1991). However, biological interactions such as competition can cause systems to be decoupled from the physical processes that determine them and can introduce both temporal and spatial lags along

with other indirect effects (Levin, 1989), causing the physical determinants to be obscured at finer scales.

The concept of scale can be defined in terms of at least two different attributes. The *grain* is the individual unit of sampling, and the *extent* is the entire geographical sampling space (Whittaker et al., 2001). Realizations about the scale-dependant nature of ecological patterns and processes have resulted in a call for a multiscale perspective, where studies are conducted at a range of scales in which grain and extent are systematically varied independently of one another (Wiens, 1989a). Most of the research investigating scale effects to date has focussed on the influence of extent alone (e.g. Mitchell et al., 2001), or else examined the influence of grain indirectly by resampling predictors derived from satellite imagery (e.g. Nams et al., 2006), ecological data (eg. Bohning- Gaese, 1997) or both to progressively coarser resolutions (Fraser, 1998; Betts et al., 2006).

In contrast, the use of different satellite sensors with varying resolutions is another way of examining how a species is “seeing” the landscape that may not be captured by resampling or increasing geographical extent alone. Further, the use of a moving window analysis may better represent how organisms experience landscape structure as pattern gradients, where the size of the moving window reflects organism perceptual abilities that may be empirically determined by varying the window size (McGarigal and Cushman, 2005). This study is unique in that it examines the effect of varying both the measurement grain, via satellite imagery of differing resolutions, and geographical extent, through a variable moving window analysis (MWA), on predicting the distribution of birds in landscapes dominated by human land uses such as agriculture

(active and regenerating fields) and suburban development (low-density housing and roads) in Eastern Ontario.

1.1 Objectives

The main goals of this study were to assess 1) the relative influences of selected grains and extents individually and 2) the important scales (i.e. combinations of grain and extent) of landscape variables for explaining bird community composition in human-dominated landscapes in Eastern Ontario.

1.2 Thesis Structure

The thesis is composed of two closely related research components which form the basis of the research objectives as outlined above. Substantial processing of satellite imagery was initially carried out to derive the landscape variables at the appropriate scales, and while not the focus of this thesis, is described in this introductory chapter in enough detail to provide the background for the main focus of the thesis. The two main research objectives of this thesis are addressed separately in Chapters 2 and 3. Chapter 2 examines the relative influences of selected grains and extents in explaining bird distribution using Canonical Correspondence Analysis (CCA) and variation partitioning, while Chapter 3 attempts to identify the important scales of landscape variables in explaining bird distribution in human-dominated landscapes of eastern Ontario using CCA models with forward selection. The concluding chapter consists of an overarching discussion and synthesis of the thesis research.

While most of the research investigating the ecological effects of scale to date has largely focussed on the influence of extent alone, it is generally assumed that landscape variables measured using a finer grain would be better to use in ecological models than

those measured with a coarser grain. I explored the assumption that finer grains will have generally better ecological predictive ability than coarser grains across variable types. I then examined the predictive ability of each type of landscape variable by scale, in light of the underlying mechanisms for which they are proxies, and current scaling research in the fields of landscape ecology and biogeography. Throughout the thesis, I express grain as metres, not metres squared, to reflect the spatial resolution of the satellite imagery. Similarly, I express extent as one side of the moving window, not the total area. For example, the 4 m spatial resolution imagery is referred to as a 4 m grain, and the 10 km X 10 km moving window as a 10 km extent.

1.3 Background

Biological diversity plays a critical role in the ecosystem services essential to humans and all life, and it is declining rapidly (Millennium Ecosystem Assessment 2005). Therefore, understanding the processes that drive species distributions is not only a key challenge of ecology (Rosenzweig, 1995) but an urgent requirement. Recently, satellite remote sensing data has been used in ecological investigations as a proxy for species diversity and distributions (Kerr and Ostrovsky, 2003) and in a wide range of biodiversity applications (Foody, 2008). By measuring the biophysical properties of environmental parameters thought to act as the driving forces underlying species distribution, remote sensing can help explain why species are found where they are. While field vegetation surveys are invaluable for collecting crucial, fine-scale habitat information necessary for wildlife and habitat management, such on-the-ground work can be both expensive and time-consuming, especially in remote regions. Remote sensing can therefore provide a useful complement for habitat characterization by providing an alternative where field work is not practical (Turner et al., 2003), and provide the consistent temporal measurements needed for monitoring purposes (Gillespie et al., 2008).

The issue of scale is particularly relevant in the use of remote sensing-derived variables in that the apparent relationship between observed patterns and the response variables often depend on the scale of mapping and rules for defining variables (Wiens, 1989a), a phenomenon known to geographers as the Modifiable Areal Unit Problem (Marceau and Hay, 1999). For example, increasing (coarsening) the grain may result in the loss of rare land cover classes that can only be resolved at finer resolutions, and may result in errors in estimates of proportions of land cover types that vary as a function of

spatial resolution (Moody and Woodcock, 1994). In addition, some remotely sensed metrics are known to exhibit non-linear scaling effects (Zhang et al., 2006).

Of the wide range of environmental parameters that have been investigated in species distribution modelling, many are particularly well-suited to detection by remote sensing. Primary productivity, climate, topography, and habitat structure measured from remotely sensed data have been applied extensively to ecological modelling scenarios (Turner et al., 2003). Remote sensing-derived land cover databases are a key component of many research applications in landscape ecology, and provide essential information about vegetation patterns and extent of anthropogenic activity (Loveland et al., 2005). This information is typically derived by identifying the spectral properties of classes of interest and assigning class labels to image pixels with these properties (Cohen and Goward, 2004).

Land cover is often used in biodiversity applications as a surrogate for habitat (Foody, 2008). For example, forest cover is an important attribute that can be gleaned from land cover that has been extensively used in wildlife habitat mapping (Cohen and Goward, 2004). Many studies have documented that forest bird richness and abundance are influenced by the amount of forest in the landscape (e.g. McGarigal and McComb, 1995; Trzcinski et al., 1999; Drapeau et al., 2000; Lee et al., 2002). Reductions in the amount of habitat have been demonstrated to have a negative impact on many biological processes crucial to species survival and persistence in the landscape such as breeding success (Kurki et al., 2000) and dispersal (With and King, 1999). In general, habitat loss has large, consistently negative effects on biodiversity, including species abundance and distribution (e.g. Best et al., 2001; Fahrig 2003).

In addition to measuring habitat amount, land cover maps can also be used to measure the spatial arrangement, or configuration, of habitat. Configuration measures such as the number of forest patches are commonly used to quantify habitat fragmentation (e.g. Trzcinski et al., 1999; Villard et al., 1999; Lichstein et al., 2002) which may be defined as the breaking up of habitat, independent of habitat loss, and results in an increase in the number of habitat patches (Fahrig, 2003). Fragmentation has been found to have both positive and negative effects on biodiversity, however, current research indicates that the amount of habitat in the landscape is generally more important than measures of fragmentation per se (Fahrig, 2003; e.g. Yaacobi et al., 2007).

While the classification of remotely sensed data into categorical maps has been important for ecological modelling studies, a more direct relationship between species and the remote sensing data is often sought through the use of vegetation indices (Turner et al., 2003; Foody, 2008). The Normalized Difference Vegetation Index (NDVI) is one remote sensing metric that has been shown to have a generally strong correlation with aboveground net primary productivity (NPP; Box et al., 1989, Phillips et al., 2008) and is one of the most commonly used and most intensively studied vegetation indices (Kerr and Ostrovsky, 2003). Kerr et al. (2001) state that measures of NPP represent a resource-based hypothesis for explaining species diversity, where plant productivity may be partitioned between species. Hurlbert and Haskell (2003) suggest that NDVI is correlated with the energy available to birds, by approximation of the productivity of the foods on which birds forage.

In addition to measures of forest amount and configuration, and productivity, remotely sensed measures of habitat heterogeneity have been used to explain species

distribution, using both land cover and reflectance data. The habitat heterogeneity hypothesis has generally been implicated using studies of species diversity, where an increase in habitat heterogeneity should lead to an increase in species diversity (MacArthur and MacArthur, 1961). Because relatively few species are found in all habitats (reflecting individual species' habitat requirements), more habitats should lead to higher species diversity (Kerr et al., 2001). Habitat heterogeneity is usually measured by quantifying discrete classes of information on the land, such as the number of land cover classes. Alternatively, the coefficient of variation of NDVI is a measure of spectral variability derived from reflectance data that has been successfully applied in the prediction of patterns of species richness at intermediate grains of 10 to 120 km at the extent of the state of Wyoming (Fraser, 1998).

1.4 Methods

1.4.1 Study Area

The study area is in Eastern Ontario, Canada, in the Thousand Islands region along the St. Lawrence River, extending roughly from Brockville, Ontario in the northeast to Kingston, Ontario in the southwest (Figure 1). The area is part of the St. Lawrence Islands National Park (SLINP) Greater Park Ecosystem (GPE) and the Frontenac Arch that connects the Canadian Shield to the Adirondack Mountains. Within the National Ecological Framework, it is part of the Mixed Wood Plains ecozone and the Frontenac Axis ecoregion (Ecological Stratification Working Group, 1996). Dominant vegetation species include sugar maple (*Acer saccharum*), eastern hemlock (*Tsuga canadensis*) and red oak (*Quercus rubra*), but the region also includes species at their northern limits (e.g. Pitch Pine (*Pinus rigida*)). Agriculture (mixed farming and dairy),

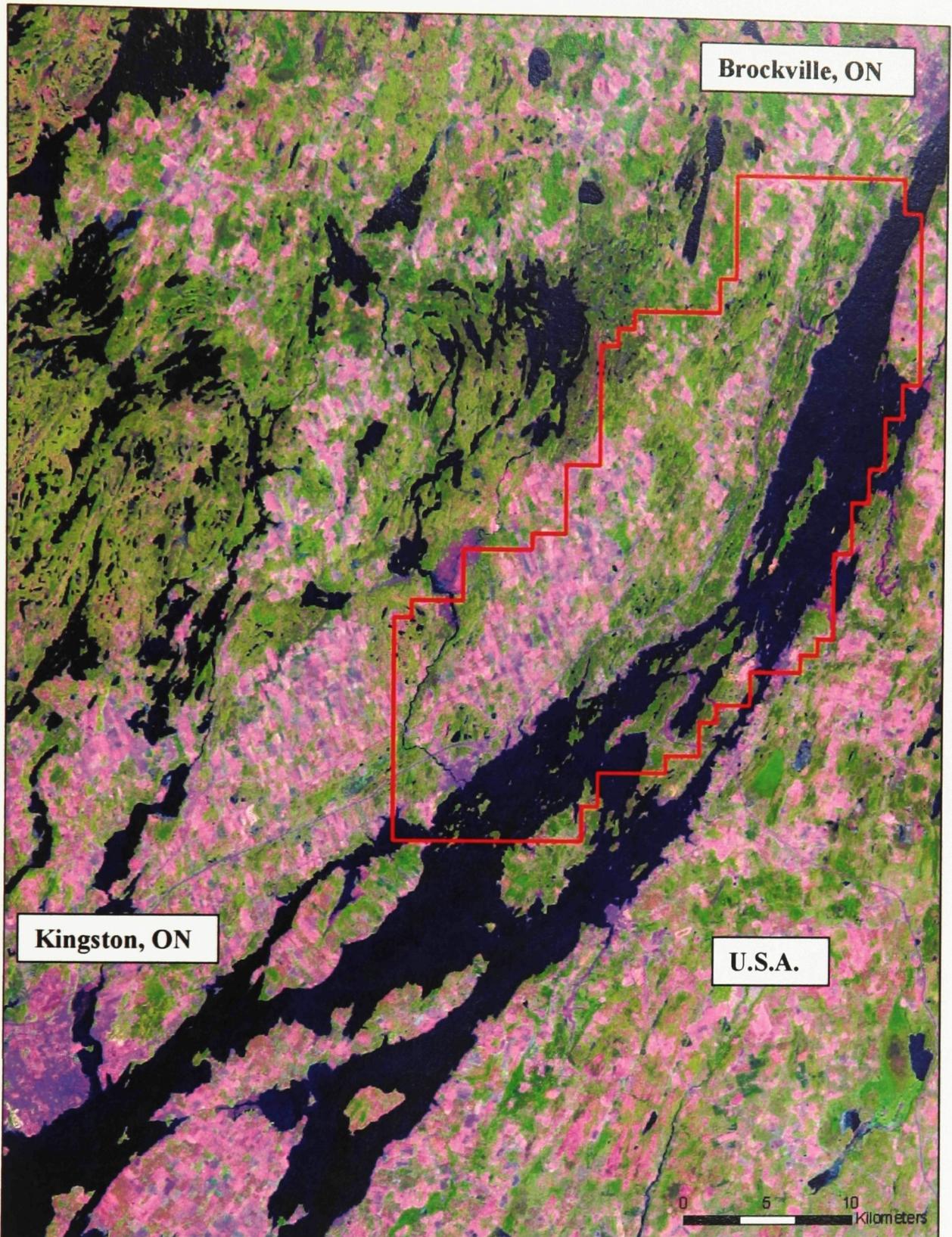


Figure 1. Location of study area in Eastern Ontario, displayed over the June 2005 Landsat image (bands 5, 4, 3). Forested areas show up as bright green, agricultural crops are mainly pink, and fallow fields and urban areas are purple.

urban development, recreation and tourism are the predominant land uses within the region.

1.4.2 Deriving Remote Sensing-based Landscape Variables

Satellite imagery was obtained from the Canada Centre for Remote Sensing (CCRS) for four satellite sensors of differing spatial resolutions: 4 m IKONOS multispectral (reflectance data only), 30 m Landsat Thematic Mapper (TM; reflectance and land cover), 250 m Moderate Resolution Imaging Spectroradiometer (MODIS; reflectance and land cover) and 1 km SPOT Vegetation (VGT; reflectance and land cover) (Table 1). The reflectance data from which the land cover products were derived were extensively pre-processed (normalized, atmospherically corrected) and land cover products were validated by CCRS (Latifovic and Olthof, 2004; Fraser et al., 2009). A Federal Geographic Data Committee (FGDC) standard vegetation legend modified specifically for the purpose of each land cover product was used (Appendix A). Since no land cover product was available for the IKONOS imagery, the mosaiced image was first clustered to 60 spectral clusters using a fuzzy K-means unsupervised clustering algorithm (Bezdek, 1973) in the PCI Geomatica v.9.0 program XPACE (PCI Geomatics, 2003), to be consistent with the methodology with which the Landsat, MODIS and VGT landcover products were created. Fuzzy K-means clustering is part of the classification by progressive generalization (CPG) methodology (Cihlar, 1999) used in combination with the enhancement classification method (ECM; Beaubien et al., 1999) by CCRS to generate the existing 3 land cover products used in this study. The 60 IKONOS clusters were subsequently merged to 30 clusters to represent the major land cover types present,

but were not labelled to land cover classes. Because the land cover was only used at the level of forest/non-forest, this likely had minimal impact on the results.

Table 1. Ancillary information for satellite imagery and land cover products used in this thesis.

Satellite	Sensor	Date(s)	Land Cover Reference
IKONOS	Multispectral	April 2000-July 2004	N/A (unpublished)
Landsat	Thematic Mapper (TM)	June 2005	Fraser et al., 2009 (CCRS)
Terra (EOS)	Moderate Resolution Imaging Spectroradiometer (MODIS)	July-August 2005 (averaged 10 day composites)	N/A – publication in preparation
SPOT	Vegetation (VGT)	April-October 2000 (averaged 10 day composites)	Latifovic et al., 2004. (CCRS)

Explanatory variable processing was carried out in Arc/INFO GRID (Environmental Systems Research Institute 2004; log file showing GRID processing steps used to process habitat variables at each spatial grain and extent is provided in Appendix B). Five explanatory variables were derived from the remote sensing imagery: number of land cover types (LC), forest amount (FS), number of forest patches (FP), mean NDVI (MN) and NDVI variability (CV)). The number of land cover types, a measure of habitat heterogeneity, was determined by simply summing the number of land cover types present within the moving window, except for the case of IKONOS data, where the number of clusters was used as surrogate for land cover types). The Landsat, MODIS, and VGT land cover products were then reclassified to the level of forest/non-forest (classes 1-15 of FGDC legend) to obtain the amount of forest and the number of forest patches. The 30 IKONOS clusters were also classified to the level of forest/non-forest, using the original IKONOS reflectance data to visually ensure that all forest was included. Forest amount was calculated as the total number of cells classified as forest,

and the number of forest patches was calculated as the total number of groups of diagonally contiguous forest cells. Mean NDVI was calculated as the average NDVI value, using the equation

$$\text{NDVI} = (\text{NIR} - \text{RED}) / (\text{NIR} + \text{RED})$$

where NIR is Near Infrared reflectance and RED is RED reflectance. NDVI variability was calculated as the coefficient of variation of NDVI, measured as the standard deviation of NDVI divided by the mean NDVI. The five variables were derived for 11 combinations of grain and extent (Table 2), for a total of 55 explanatory variables. Variables were not derived for IKONOS extents larger than 250 m, and Landsat extents larger than 5 km, after initial testing revealed that a lengthy processing time would be involved for such extensive spatial operations. Figure 2 provides a visual comparison of selected variable grains and extents over a portion of the study area.

Table 2. Combinations of grain (spatial resolution) and extent (one side of moving window) used to derive the explanatory variables in this study. Colored boxes indicate groupings of variables used for analysis in Chapter 2.

Satellite/Sensor	Grain	Extent				
		90 m	250 m	1 km	5 km	10 km
Ikonos	4 m	X	X			
LandsatTM	30 m	X	X	X	X	
MODIS	250 m			X	X	X
SPOT VGT	1 km				X	X

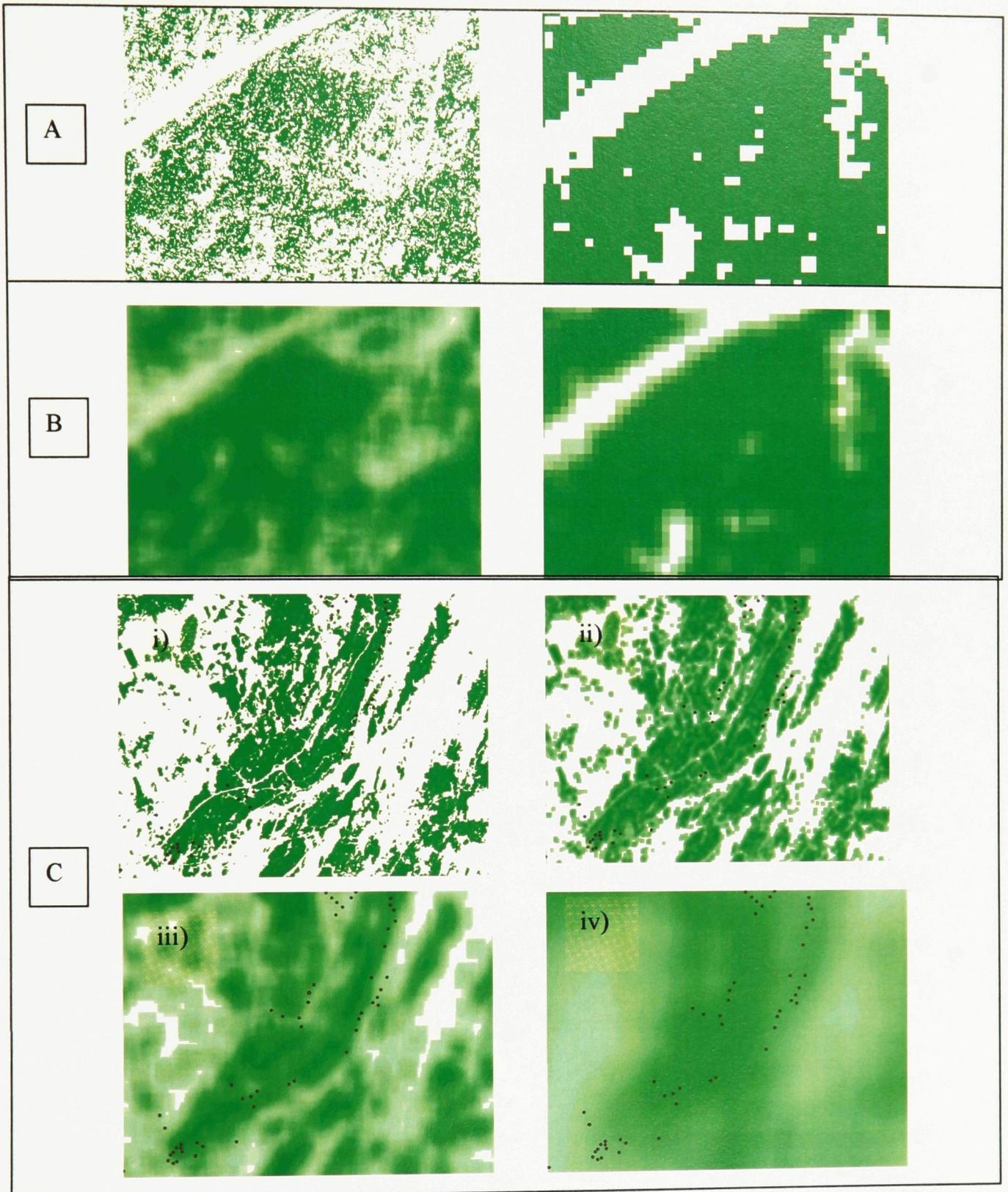


Figure 2. Visual comparison of variables measured over part of the study area. The 4 m grain (left pane) and 30 m grain (right pane) are compared in Boxes A, forested (green) and non-forest (white) and B, the amount of forest at a 90 m extent). Box C shows a 30 m grain Moving Window result for forest amount at (i) 90 m ii) 250 m iii) 1 km and iv) 5 km extents. Values of variables were sampled at bird survey locations shown in red.

1.4.3 Bird surveys

Bird survey sites were chosen to maximize the variation present in the environmental variables, by using a k-means unsupervised cluster image of all landscape variables at all grains and extents. The 55 explanatory variable grids were entered into a k-means unsupervised clustering algorithm in PCI XPACE (PCI Geomatics, 2003). K-means is a type of clustering algorithm used to determine the natural statistical groupings present in the data set (Lillesand and Keifer, 2000). Bird surveys were limited to a section of the study area with overlapping extents for all imagery, to ensure explanatory variables could be derived for the same geographic area. Bird species presence/absence was sampled at 95 sites throughout SLINP and GPE by single 10-minute, unlimited distance point counts following standardized bird sampling protocol (Ralph et al., 1995), between June 12 and 20, 2007.

Bird surveys were mainly road-based, selecting only for secondary and tertiary roads, with special care to minimize noise effects from Highway 401, although some sampling also took place on hiking trails. Birds flying high over head such as gulls and herons that did not appear to be using the habitat were recorded separately. Figure 3 shows the location of bird sampling sites throughout the study area.

1.4.4 Environmental variable sampling

The values of all 55 predictor variable grids (5 variables measured at 11 scales (Table 2)) were measured at the locations of the bird sampling sites (N=95), using the Sample function in GRID. The nearest neighbour assignment resampling algorithm was used to assign a value from each of the 55 variables under the locations of bird points, because it

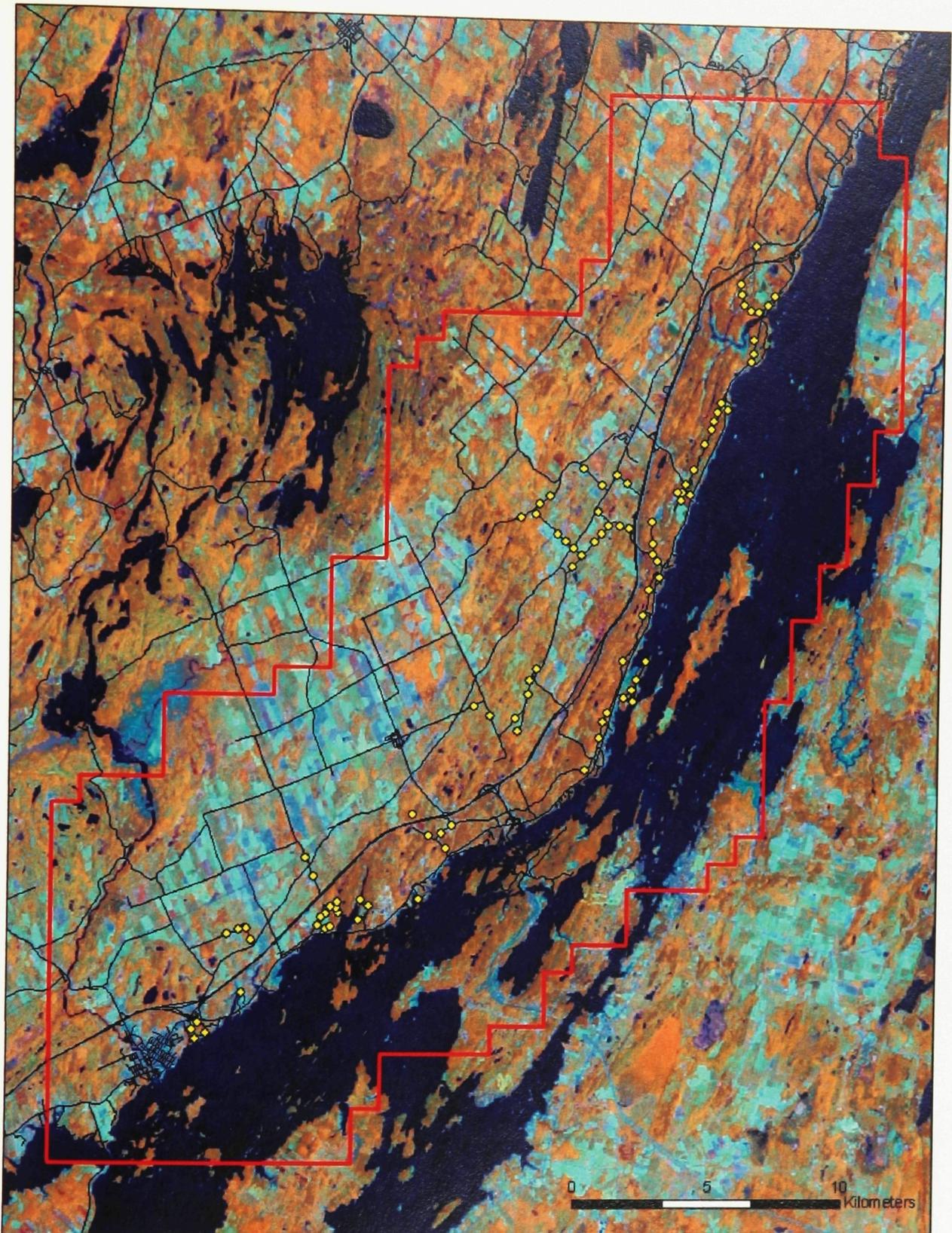


Figure 3. Distribution of 95 bird survey points (yellow) within the study area, displayed on the June 2005 Landsat imagery (bands 4,5,3). Major roads are shown in black.

does not alter the value from the input grid cells to the resampled grid cells (Environmental Systems Research Institute, 2004).

1.4.5 Testing for Spatial Autocorrelation

Positive spatial autocorrelation (SA) in species distribution data occurs when nearby points in space are more similar than pairs of random points. SA may be caused by biological processes such as geographic dispersal or social organization that are related to distance or by omitting spatially structured environmental factors (Legendre and Fortin, 1989). However, a failure to account for SA in the response variable violates the assumption of independence and may inflate the Type 1 error rate (Dormann et al., 2007). The species-environment relationships in this thesis were assessed using CCA, a multivariate regression analysis that assumes that the species and sampling units are independent (Wagner, 2004). I therefore measured the amount of SA in the species data using a Mantel (1967) test on geographic distance, to answer the question “are samples that are close together also compositionally similar?” (Urban et al., 2002). The Mantel test evaluates the null hypothesis of no relationship between two dissimilarity matrices (McCune and Mefford, 1999). The bird species data were therefore arranged into a species by sites matrix, and converted to Sorensen’s Index, a multivariate index of overall species similarity (Sorensen, 1948) and a geographic distance matrix was calculated for the bird sampling points. Pearson’s correlation, known as the standardized Mantel statistic (r) in this context (Sokal and Rohlf, 1995), was used as a measure of the strength between the two distance matrices. However, the significance of the correlation was evaluated using a Monte Carlo randomization procedure with 1000 permutations, because

the cells of distance matrices are not independent of each other. All steps in this section were conducted using the computer program PC-ORD (McCune and Mefford, 1999).

1.5 Results

1.5.1 Bird Species Community

A total of 84 bird species were detected and species richness varied between 6 and 17 species per survey point. The bird species most commonly detected were red-winged blackbird, American robin and American goldfinch (Table 3). All ducks, gulls, herons and other species deemed to not be using the habitat were excluded from the analyses, as well as species present at less than 10% of sites, because uncommon species are not suitable for inclusion in CCA (ter Braak and Smilauer, 2002). Chipping sparrow and pine warbler were also excluded due to identification difficulty, leaving 33 species for the analyses in Chapters 2 and 3.

1.5.2 Distribution of landscape variables at bird sample points

Summary statistics (mean, coefficient of variation) for explanatory variables at each scale can be found in Appendix C. Due to the large file size, the correlations for all 55 variables are provided separately as an electronic appendix (Appendix E).

1.5.3 Spatial Autocorrelation

An extremely low, yet significant level of spatial autocorrelation was detected in the bird species data (Mantel's $r = 0.065$, $p = 0.023$), indicating that sites closer together were more similar in terms of species composition than sites farther apart. However, a level of spatial autocorrelation this low may be biologically unimportant and likely only had minimal impact on the analyses.

Table 3. Name and relative frequency of the 33 bird species included in, and 51 species excluded from the analyses. Relative frequency was calculated as the number of sites detected divided by the total number of sites surveyed (n=95).

Common Name	Scientific Name	Code	Number of sites detected	Relative Frequency
American Crow	<i>Corvus brachyrhynchos</i>	AMCR	46	0.48
American Goldfinch	<i>Carduelis tristis</i>	AMGO	60	0.63
American Redstart	<i>Setophaga ruticilla</i>	AMRE	26	0.27
American Robin	<i>Turdus migratorius</i>	AMRO	63	0.66
Baltimore Oriole	<i>Icterus galbula</i>	BAOR	29	0.31
Bank Swallow	<i>Riparia riparia</i>	BANS	14	0.15
Black-capped Chickadee	<i>Poecile atricapillus</i>	BCCH	32	0.34
Brown-headed Cowbird	<i>Molothrus ater</i>	BHCO	16	0.17
Blue Jay	<i>Cyanocitta cristata</i>	BLJA	40	0.42
Bobolink	<i>Dolichonyx oryzivorus</i>	BOBO	13	0.14
Cedar Waxwing	<i>Bombycilla cedrorum</i>	CEDW	11	0.12
Common Grackle	<i>Quiscalus quiscula</i>	COGR	34	0.36
Common Yellowthroat	<i>Geothlypis trichas</i>	COYE	57	0.60
Eastern Kingbird	<i>Tyrannus tyrannus</i>	EAKI	16	0.17
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	EATO	10	0.11
European Starling	<i>Sturnus vulgaris</i>	EUST	23	0.24
Eastern Wood-Peevee	<i>Contopus virens</i>	EWPE	16	0.17
Great-crested Flycatcher	<i>Myiarchus crinitus</i>	GCFL	9	0.09
Gray Catbird	<i>Dumetella carolinensis</i>	GRCA	20	0.21
House Wren	<i>Troglodytes aedon</i>	HOWR	39	0.41
Mourning Dove	<i>Zenaida macroura</i>	MODO	32	0.34
Northern Cardinal	<i>Cardinalis cardinalis</i>	NOCA	10	0.11
Ovenbird	<i>Seiurus aurocapillus</i>	OVEN	20	0.21
Red-eyed Vireo	<i>Vireo olivaceus</i>	REVI	41	0.43
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	RWBL	66	0.69
Savannah Sparrow	<i>Passerculus sandwichensis</i>	SASP	10	0.11
Song Sparrow	<i>Melospiza melodia</i>	SOSP	59	0.62
Tree Swallow	<i>Tachycineta bicolor</i>	TRES	13	0.14
Veery	<i>Catharus fuscescens</i>	VEER	11	0.12
Warbling Vireo	<i>Vireo gilvus</i>	WAVI	24	0.25
White-breasted Nuthatch	<i>Sitta carolinensis</i>	WBNU	13	0.14
Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	YBSA	10	0.11
Yellow Warbler	<i>Dendroica petechia</i>	YEWA	56	0.59

Species detected but excluded from the analyses.

Common Name	Scientific Name	Code	Number of sites present	Relative Frequency
Barn Swallow	<i>Hirundo rustica</i>	BNSW	4	0.04
Black-and-white Warbler	<i>Mniotilta varia</i>	BWWA	8	0.08
Black-throated Green Warbler	<i>Dendroica virens</i>	BTGN	3	0.03
Blue-headed Vireo	<i>Vireo solitarius</i>	BHVI	3	0.03
Brown Creeper	<i>Certhia Americana</i>	BRCR	2	0.02
Brown Thrasher	<i>Toxostoma rufum</i>	BRTH	2	0.02
Canada Goose	<i>Branta Canadensis</i>	CAGO	3	0.03

Chestnut-sided Warbler	<i>Dendroica pensylvanica</i>	CSWA	3	0.03
Cliff Swallow	<i>Petrochelidon pyrrhonota</i>	CLSW	3	0.03
Common Raven	<i>Corvus corax</i>	CORA	1	0.01
Common Snipe	<i>Gallinago gallinago</i>	COSN	5	0.05
Common Tern	<i>Sterna hirundo</i>	COTE	1	0.01
Downy Woodpecker	<i>Picoides pubescens</i>	DOWO	9	0.09
Eastern Meadowlark	<i>Sturnella magna</i>	EAME	7	0.07
Field Sparrow	<i>Spizella pusilla</i>	FISP	3	0.03
Golden-crowned Kinglet	<i>Regulus satrapa</i>	GCKI	1	0.01
Great Blue Heron	<i>Ardea herodias</i>	GBHE	7	0.07
Green Heron	<i>Butorides virescens</i>	GRHE	3	0.03
Hairy Woodpecker	<i>Picoides villosus</i>	HAWO	5	0.05
Hermit Thrush	<i>Catharus guttatus</i>	HETH	1	0.01
Herring Gull	<i>Larus argentatus</i>	HEGU	6	0.06
House Finch	<i>Carpodacus mexicanus</i>	HOFI	2	0.02
House Sparrow	<i>Passer domesticus</i>	HOSP	4	0.04
Indigo Bunting	<i>Passerina cyanea</i>	INBU	2	0.02
Killdeer	<i>Charadrius vociferous</i>	KILL	5	0.05
Least Flycatcher	<i>Empidonax minimus</i>	LEFL	1	0.01
Mallard	<i>Anas platyrhynchos</i>	MALL	1	0.01
Nashville Warbler	<i>Vermivora ruficapilla</i>	NAWA	4	0.04
Northern Flicker	<i>Colaptes auratus</i>	NOFL	3	0.03
Northern Waterthrush	<i>Seiurus noveboracensis</i>	NOWA	1	0.01
Osprey	<i>Pandion haliaetus</i>	OSPR	1	0.01
Pileated Woodpecker	<i>Dryocopus pileatus</i>	PIWO	6	0.06
Purple Finch	<i>Carpodacus purpureus</i>	PUFI	3	0.03
Red-breasted Nuthatch	<i>Sitta Canadensis</i>	RBNU	4	0.04
Red-tailed Hawk	<i>Buteo jamaicensis</i>	RTHA	2	0.02
Ring-necked Pheasant	<i>Phasianus colchicus</i>	EAPH	4	0.04
Rock Pigeon	<i>Columba livia</i>	RODO	3	0.03
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	RBGR	5	0.05
Ruby-throated Hummingbird	<i>Archilochus colubris</i>	RTHU	2	0.02
Ruffed Grouse	<i>Bonasa umbellus</i>	RUGR	2	0.02
Scarlet Tanager	<i>Piranga olivacea</i>	SCTA	7	0.07
Sharp-shinned Hawk	<i>Accipiter striatus</i>	SSHA	1	0.01
Swamp Sparrow	<i>Melospiza Georgiana</i>	SWSP	4	0.04
Turkey Vulture	<i>Cathartes aura</i>	TUVU	3	0.03
Vesper Sparrow	<i>Pooecetes gramineus</i>	VESP	7	0.07
Wild Turkey	<i>Meleagris gallopavo</i>	WITU	1	0.01
Willow Flycatcher	<i>Empidonax traillii</i>	WIFL	2	0.02
Wood Thrush	<i>Hylocichla mustelina</i>	WOTH	7	0.07
Yellow-rumped Warbler	<i>Dendroica coronata</i>	YRWA	4	0.04
Chipping Sparrow/ Pine Warbler	<i>Spizella passerine/</i> <i>Dendroica pinus</i>	CHSP/ PIWA	40	0.42

2 RELATIVE INFLUENCE OF GRAIN AND EXTENT

2.1 Background

The concept of scale can be defined in terms of at least two different attributes: (1) the *grain*, or the individual unit of sampling, and (2) *extent*, which is the entire geographical sampling space (Whittaker et al., 2001). While the geographical extent of a study is often referred to as the scale, this is an incomplete definition, since it ignores the grain (Wiens 1989; Mitchell et al., 2001). Further, it may have more ecological meaning to define grain and extent from the perspective of the organism being studied (McGarigal and Marks, 1995). However, choosing an appropriate scale for analysis may be difficult if basic life history information, such as dispersal, is unknown, and because scale is a continuous property (Cushman and McGarigal, 2004).

Changing the scale used to measure an explanatory variable will affect how strongly an organism responds, depending on whether grain, extent or both are changed. When extent is held constant, an increase in grain generally decreases spatial variance, because a larger portion of the spatial heterogeneity is contained within the sample. Smaller individual landscape elements that could previously be differentiated are now averaged out and are lost. When the grain is held constant, an increase in extent generally increases spatial variance because new landscape elements that were not initially present may be encountered, increasing the spatial heterogeneity (Wiens, 1989). Accordingly, the tradeoff between grain and extent that researchers often face when using satellite imagery is that while more information is inherent in higher-resolution data, it comes at the price of increased variability. On the other hand, coarser resolution images may have mixed-pixel problems (Rochinni, 2007). The choice of scale is complicated by the fact that usually, smaller extents are measured in finer resolution, while for logistical reasons

larger extents are measured with coarser resolution (Wiens, 1989). The challenge in the use of both remote sensing and ecological data at multiple scales is to retain the essential information without getting bogged down in unnecessary detail (Levin, 1992).

In a review of avian modeling studies using remote sensing imagery, Gottschalk et al. (2005) noted that although the selection of the 'right' satellite sensor is an important decision that affects the outcome of the described wildlife-habitat relationship, no detailed methods are available to provide guidance on such decisions. Further, the 109 reviewed studies showed few considerations in regards to spatial scale and choice of appropriate satellite sensor, emphasizing the choice of spatial scale(s) is often ignored in bird-habitat modeling studies. The series of Landsat sensors, with a 30m spatial resolution, is the most widely used sensor for biodiversity studies (Gillespie et al., 2008) and in modeling avian habitat relationships with satellite imagery (Gottschalk et al., 2005). The relatively high spatial resolution, low cost, long time-series (30+ years), and wide availability are likely the reasons why it has seen such extensive use (Gillespie et al., 2008). However, studies mapping bird species distributions have also found grains of 250 m (Luoto et al., 2004), 1.1 km (Lawler et al., 2004) and 5-10 km (Venier et al., 2004) appropriate. Few studies have directly compared the explanatory ability among different grains. Rocchini (2007) compared the effectiveness of 4 spatial resolutions ranging from 4 m to 60 m in predicting plant ecosystem diversity using measures of image heterogeneity, and found that while the finest resolution was highly correlated ($r = 0.67$), so were both 30 m Landsat ($r = 0.67$) and Landsat resampled to 60 m ($r = 0.69$).

Based on the rationale that little is known about landscape scales governing habitat selection in birds, Mitchell et al. (2001) evaluated concentric landscape extents

around bird survey points ranging from 80 m to 3000 m radii, and found that the mean scale of landscape variables based on forest age and type was unrelated to successional class, migratory status, or degree of habitat specialization. They concluded that it is unlikely that any single scale can be used to assess landscape characteristics for any coarse ecological groupings of bird species. Other studies on forest age and cover type (e.g. Drapeau et al., 2000; Betts et al., 2006) have found extents ranging from 500-2000 m to influence forest bird abundance.

For the range of grains and extents measured in this study, it was expected that the finer grains would explain more information about the bird community than coarser grains in general, and that overall, changing the grain would explain a much higher proportion of the variation in the bird data than changing the extent, both as a result of a greater amount of spatial heterogeneity information in the higher resolution imagery, and also because the range of grains are closer to the scales at which birds directly interact with their environment.

2.2 *Methods*

2.2.1 Canonical Correspondence Analysis and Variation Partitioning

Variation partitioning is a relatively common ecological analysis technique that has been applied in several different contexts. Borcard et al. (1992) first demonstrated the use of canonical ordinations to partition the variation among environmental and spatial components of community data sets. A matrix of environmental variables is used to constrain the amount of variation explained in the species matrix, while a matrix of covariables can be used to ‘partial out’ the effects of variables from the analysis. This methodology has since been extended to include a temporal component (Anderson and

Gribble, 1998) and has been used to partition the effects of habitat and farm practices on bird species composition (Freemark and Kirk, 2001) as well as multi-scale hierarchical relationships (Cushman and McGarigal, 2004).

In this study, multivariate ordination was used to partition the variation in the species data by the different grains and extents because it allows the full suite of species information to be used and surpasses the problem of insufficient data for individual species regression models (ter Braak and Smilauer, 2002). Canonical Correspondence Analysis (CCA; ter Braak, 1986) using the computer software Canoco for Windows 4.5 (ter Braak and Smilauer, 2002) was used because a range of 1.5 to 3 standard deviations on the axis of the first environmental gradient is considered acceptable for either a unimodal (CCA) or linear (Redundancy Analysis; RDA) species response model (ter Braak and Prentice, 1988). A Detrended Correspondence Analysis on the species matrix revealed a gradient length of 2.45.

The environmental variables were first divided into three groupings of variables measured at common extents, in order to avoid confounding effects from different extents. For example, 4 m and 30 m grain variables were both measured at 90 m and 250 m extents and thus included in the same group of variation partitioning models (Table 2, referred to in this section as fine grain/small extent models). First, a CCA of all 4 m grain variables measured at both 90 m and 250 m extents was carried out to determine the total amount of variation explained. In Canoco, explanatory variables can be entered into models as covariables to adjust for the effect on the species data, eliminating their effect in the resulting partial ordination (ter Braak and Prentice, 1988). The second step was a partial CCA with the same variable set, to determine the importance of the 4 m grain,

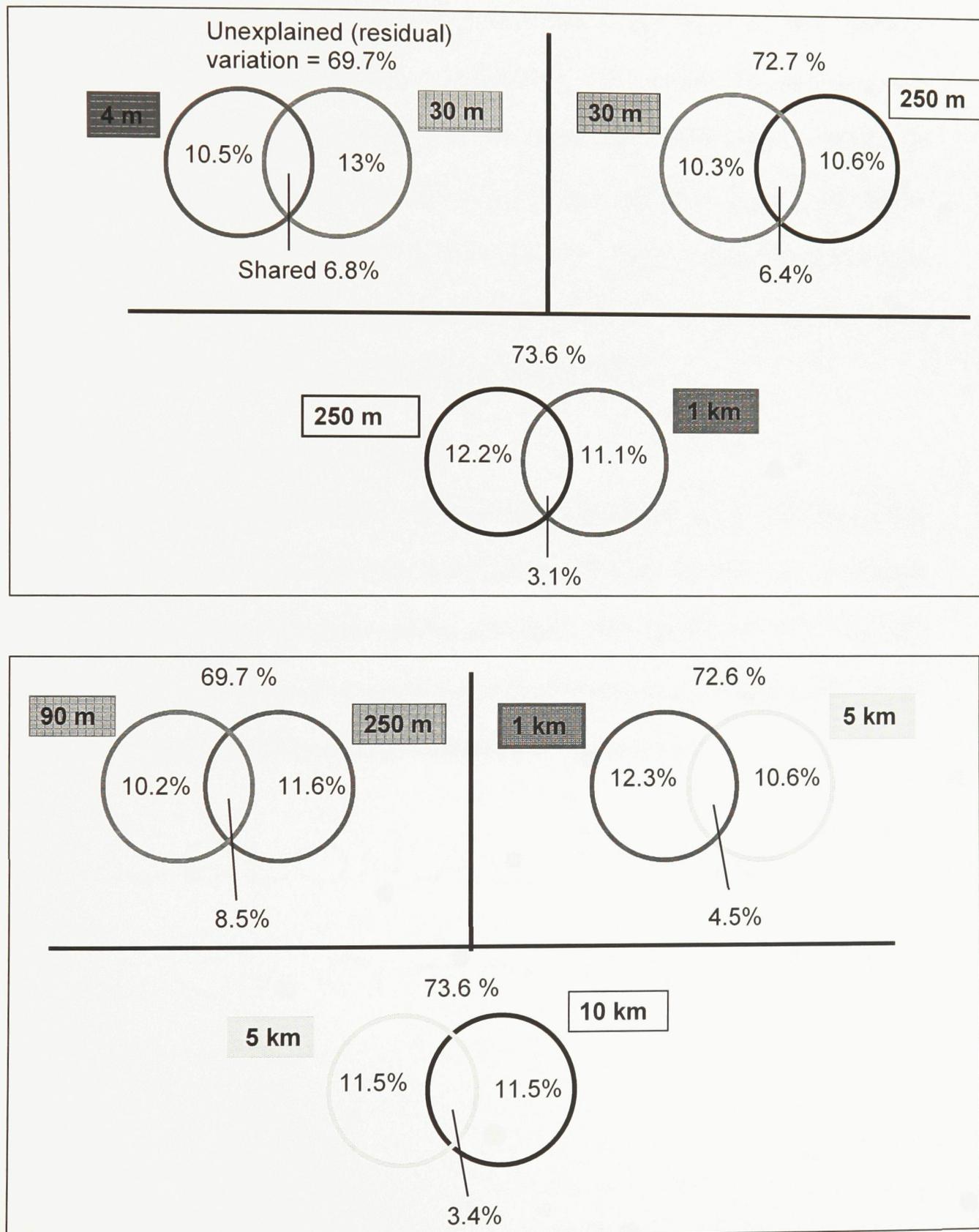
where the 30 m grain variables of the same extents were entered as covariables. This step reveals the unique variation explained by the 4 m grain that is remaining when the variation that can be explained by the 30 m grain is taken into account. This partial CCA is crucial because otherwise, it is unknown what proportion of the total variation explained is actually due to the 4 m grain, since some of the variation that is measured by the 4 m grain is also being measured by the 30 m grain. To examine the influence of extent, a reciprocal approach that kept grain constant was then used: a CCA on all 90 m extent variables (measured with both 4 m and 30 m grains) was carried out to determine the total variation explained, and then a partial CCA was run on the same variables by entering the 250 m extent variables as covariables. The above process was repeated for the other two groups of grain and extents in Table 2, referred to as the medium grain/medium extent and coarse grain/large extent models. For each model, Monte Carlo tests (Manly, 1990) with 999 permutations were used to test for significance.

2.3 Results

2.3.1 Grain

Overall, there was little difference among both the total and unique variation explained among variable grains. The highest unique variation explained (UVE; 13%) was from 30 m grain variables in the fine grain model, although all variable grains explained at least 10.3% (Figure 4). The full fine grain model explained more total variation (TVE; ~30%) than medium or coarse grain models (~26%). Shared variation (the total variation minus unique variation) was quite low for the coarse grain models (250 m and 1 km; ~3%), while medium (30 m and 250 m) and fine grain (4 m and 30 m) models both shared roughly 7% (Table 4).

Figure 4. Venn diagram illustrating results from variation partitioning by variable grains (top 3 graphics) and extents (bottom 3 graphics). Variable grains or extents tested (colored boxes outside the circles) and the amounts of unique variation explained by each are given within the circle of the same color.



2.3.2 Extent

Similar to the grain models, there were slight differences in total variation explained by extent model groupings. A decrease in total variation explained was seen when moving from smaller (17-20% TVE) to larger (15% TVE) extents. While the unique variation explained was similar across extents, variables at the 1 km extent explained the most unique variation (12.3%; Figure 4). Shared variation was also quite low for the large (5 km and 10 km) and medium (1 km and 5 km) extent models (3-5%) and slightly higher for variables at the smallest extents (~8.6%).

2.3.3 Contribution of Grain vs. Extent

For all 3 model subsets, UVE by both variable grain and extent was very similar (between 10.2 % and 13%; Table 5). Although the TVE by variable grain and extent differed slightly between the three variable groupings, within groups there was very little difference. Variables at the 30 m grain explained the most unique variation (13%) in the bird data out of all variable grains and extents that were examined.

Table 4. Results of partitioning variation in bird species data by grain and extent of explanatory variables.

Model variables	Covariables	Total Variation ^a (%)	Unique Variation ^b (%)	Shared Variation ^c (%)
4 m grain	30 m grain (both extents)	17.35	10.50	6.85
30 m grain**	4 m grain (both extents)	19.78	13.00	6.78
90 m extent	250 m extent (both grains)	18.78	10.20	8.58
250 m extent*	90 m extent (both grains)	20.17	11.60	8.57
Full model (all grains and extents in group)**		30.35		
30 m grain	250 m grain (both extents)	17.00	10.30	6.40
250 m grain*	30 m grain (both extents)	17.09	10.60	6.49
1 km extent**	5 km extent (both grains)	16.83	12.30	4.53
5 km extent	1 km extent (both grains)	15.09	10.60	4.49
Full model**		28.39		
250 m grain**	1 km grain (both extents)	15.30	12.20	3.10
1 km grain*	250 m grain (both extents)	14.22	11.10	3.12
5 km extent**	10 km extent (both grains)	14.91	11.50	3.41
10 km extent**	5 km extent (both grains)	14.91	11.50	3.41
Full model**		26.48		

^a Total Variation = The total variation in the species data explained by a CCA of the model's explanatory variables in the first column

^b Unique Variation = The variation that can be explained by the model variables after partialling out the effect of the covariables in the second column

^c Shared Variation = Total Variation - Unique Variation; ie. The amount of variation shared between model variables and covariables

* $P \leq 0.05$ ** $P \leq 0.01$. All models without covariables were significant at $P \leq 0.001$

2.4 Discussion

The results of the variation partitioning analysis indicate that, for the landscapes and landscape variables that were sampled in this study, there is little difference in amount of variation explained by the variable grains and extents examined. This finding is somewhat surprising for several reasons. First, it was expected that the finer grains would explain more variation in the bird data than the coarser grains since they more closely approximate territory size and therefore the resolution at which birds might be perceiving the landscape. Although finer-grained variables did explain more variation in the bird community in this study, it was only by a small margin. However, some studies

have found that an increase in spatial resolution does not necessarily always translate directly to an increase in variance explained (e.g. Rocchini, 2007). Statistical methods such as those outlined in Peres-Neto et al. (2006) must be used to determine if differences between the amount of variation explained by variable grains and extents are statistically significant. Second, many studies have noted a scaling effect in which the strength of the response varied depending on the extent of the analysis window (e.g. Nams et al., 2006; Betts et al., 2006; Smith et al., 2008). Although only extents within subgroups were directly compared, there were only small differences among any of the extents examined. Overall, the variable extents examined explained as much variation in the bird species data as the variable grains that were examined.

One potentially important constraint imposed by the variation partitioning methodology used here was that small grains were not directly compared to larger grains in the same model. It seems likely that, were it possible to partition the variation in the bird data across all grains and extents examined, a larger difference would be detected, especially between fine and coarse grain variable. Unfortunately, such an analysis was not possible because the fine-grained variables were only produced at smallest extents due to processing time constraints, thus constraining the extent in comparisons to larger grains.

While the amount of unexplained variation for all grain/extent models was relatively high in relation to the total amount of variation explained, this is quite common in the literature (Borcard et al., 1992) and indicates that although some of the grains and extents for the measured variables are important to birds, there is at least one, but likely several other unmeasured factors influencing the bird community composition. Some

may be microscale environmental factors (e.g. snags) that cannot even be detected at the smallest grain/extents. Additionally, variation may be due to other elements that cannot easily be measured environmentally, where links among organisms such as competition or predation are responsible for community structure (Southwood, 1987).

2.4.1 Conservation recommendations/Limitations

There was not much difference in the variation explained by the 5 variables at the grains and extents examined. It would be highly beneficial for conservation organizations with limited budgets if 30 m was just as good as higher resolution, because of cost considerations alone, however, further investigation across a greater environmental gradient is required before more certain generalizations can be made.

In the current study, although the bird survey design was guided by the landscape variable clusters in an effort to ensure the full range of variation in the variables was sampled, it is possible that the extent of the study area itself was simply too small to capture a large enough range in the environment to adequately differentiate the importance of grain compared to extent. For example, the 5 km extent measured with the 1 km grain is only 5 pixels by 5 pixels in area. Here, the area under examination was predetermined based on the area of overlapping imagery extents, which was ultimately limited by the small extent of the IKONOS imagery that was available. Repeating the current study at a larger scale using commercial satellite imagery such as IKONOS would likely be prohibitively expensive, in addition to requiring enormous amounts of data processing time. However, recently available sources of free, pre-processed Landsat and other medium to coarse resolution satellite products open up new possibilities for comparisons of ecological modelling variable grain and extent within North America.

3 IMPORTANT SCALES OF INDIVIDUAL EXPLANATORY VARIABLES

3.1 *Background*

Spatial patterns of bird richness and distribution may be due to the combination of large-scale biogeographical variation and fine scale ecological variation (Wiens 1989b). Most studies of habitat associations occur at relatively fine scales, while the processes that determine them may occur on a much broader scale, making it difficult to match pattern to process (Levin, 1992). Further, it is generally accepted that individual species select habitat hierarchically, starting with the geographical region (first-order) of a species to nest site selection (fourth-order) (Johnson, 1980). Because species respond to multiple scales of gradients of environmental heterogeneity individually (Wiens, 1989a) community-level species-environment relationships should be considered at a range of scales simultaneously (Cushman and McGarigal, 2004).

Numerous studies have indicated that the amount of forest on the landscape is one of the most important predictors of individual bird species presence and/or forest bird community composition (e.g. McGarigal and McComb 1995; Trzcinski et al., 1999; Drapeau et al., 2000). However, the response may vary with the scale of investigation, and depend on the individual species (Lee et al., 2002) and/or the matrix surrounding the forest (Dunford and Freemark, 2004). For example, Bohning-Gaese (1997) studied bird species richness in central Europe in an area of mixed land use and found that forest area decreased in predictor importance as the quadrat examined increased from 2 km to 6 km. The author explained this difference as being due to high within-habitat spatial heterogeneity within 2 km. However, a study by Trzcinski et al. (1999) found that forest cover was positively related to 33 species of forest birds in predominantly agricultural

areas of southern Ontario and Quebec at a resolution of 10 km. Because habitat loss has important implications at most scales that have been examined, I expected the amount of forest would be important for predicting bird community composition, regardless of scale.

Studies seeking to separate the influence of forest configuration after accounting for habitat amount have generally found less of an effect of configuration. One study near Ottawa, ON, by Villard et al. (1999) quantified forest fragmentation as the number of forest fragments (in addition to other measures of configuration). After controlling for habitat amount, they found a significant effect of forest fragmentation at the 2.5 km grain/10km extent. They concede however, that this effect may have been due to increased sampling effort in fragmented landscapes.

Support for habitat heterogeneity as an important predictor of bird assemblages and species richness has been found at the patch scale (Freemark and Merriam, 1986) and the landscape scale for grains of 2-6 km (Bohning-Gaese, 1997) in central Europe. Fraser (1998) found species richness in Wyoming to be more strongly influenced by several measures of environmental heterogeneity, such as number of cover types and NDVI variability, than measures of climatic energy or primary productivity using sampling grains of 10-120 km. In contrast, a recent study by Coops et al. (2009) over Ontario using a 10 km grain did not find within cell habitat heterogeneity, calculated as the coefficient of variation of NDVI, to be an important predictor of bird species richness or habitat and nesting guilds. Since the role of habitat heterogeneity has been established at both fine and coarser grains, it was expected that variables measuring habitat heterogeneity at both fine and coarse grains would likely be important to birds.

Most ecological studies that have used the Normalized Difference Vegetation Index (NDVI) have done so at the scale of regions or continents (e.g. Hurlbert and Haskell, 2003). However, Phillips et al., (2008) found a very strong relationship between NDVI and bird richness using a 1 km grain. Seto et al., (2004) measured the ability of mean and maximum NDVI to predict bird and butterfly species richness using grains based on canyon and sub-divisions of the canyon based on 100 m changes in elevation. They found the strongest relationship for larger grains and extent for birds, but smaller grains for butterflies, which they hypothesize may be due to differences in home range sizes. Overall, there is no consensus on what scale NDVI should be measured at for species distribution modelling (Gillespie et al., 2008), however, NDVI seems to be important at larger scales, presumably due to its strong correlations with productivity, which has also been implicated at coarse scales.

3.2 Methods

3.2.1 Ranking of variables using forward selection

Including too many variables can artificially increase the amount of variation explained due to multicollinearity (Cushman and McGarigal, 2004). The number of landscape variables from the original suite of 55 was therefore reduced to a smaller subset by CCA with forward selection. Variables were first grouped by the 5 variable types (forest amount, number of forest patches, etc.) and subjected to the stepwise forward selection procedure in CCA, so that all variable types were initially treated equally (Appendix D). A final CCA model that retained only the significant ($P < 0.05$) variables from the models of each variable type ($n=20$), using forward selection was used

to rank the importance of individual variables. Monte Carlo tests with 999 permutations were used to test for significance.

3.2.2 Ordination diagram

To assess species-habitat relationships, an ordination diagram of species and the significant environmental variables from the final CCA model was plotted using CanoDraw (ter Braak and Smilauer, 2002). Ordination diagrams are a means of visualizing the relationships between multivariate species and environmental data and are the primary method for presenting the results of ordination models (Leps and Smilauer, 2007). Species scores are shown by points and environmental variables are represented by arrows, with their relative length directly proportional to their importance to community structure (ter Braak, 1986). The arrangement of species and environmental variables in ordination space is such that similar entities are close by and dissimilar entities are farther apart (Gauch, 1982).

3.3 Results

3.3.1 Importance of variable types

The initial forward selection procedure, stratified by variable type, resulted in the retention of 20 significant variables for entry into the final model (Appendix D). Four variables were significant for each type of variable, except for the number of land cover types and number of forest patches, which had three and five significant variables respectively. After running the final model with all 20 significant variables, 8 variables remained significant at the $P < 0.05$ level, and all variable types had at least one variable that was significant (Table 5), explaining 48% of the variation in the bird data. The top two ranked variables were both measures of forest amount; the highest amount of

Table 5. Significant variables resulting from final CCA model, after reducing variable set with forward selection by variable type. Variables (with their respective grain/extents) are listed in order of their inclusion in the model, with the additional variance explained by its inclusion, and its associated significance as determined by Monte-Carlo tests (999 permutations; P).

Variable	Grain (m)	Extent (m)	Variance Explained	P
Forest amount	4	90	0.14	0.001
Forest amount	30	1000	0.07	0.001
Number of land cover types	30	250	0.06	0.001
Mean NDVI	30	90	0.05	0.001
NDVI Variability	1000	10000	0.05	0.002
Number of forest patches	250	5000	0.04	0.003
Number of forest patches	4	250	0.04	0.023
Mean NDVI	30	1000	0.03	0.045
			Total = 0.48	

variance explained by far was from the 4 m grain and 90 m extent (0.14) followed by the 30 m grain measured at the 1 km extent (0.07), for a total of 0.21, or nearly half of the total variance explained by the significant landscape variables, and 34% explained by all variables in the final model. The remaining significant variables were a mix of variable type, grain and extent, with the other variable types explaining about an equal proportion of the total variance. A full two thirds of the significant variables were measures of forest amount, explaining a quarter of the total variation in the bird community. Correlations between the 20 variables in the final model were generally low, with the exception of several variables (Table 6). Mean NDVI measured with the 30 m grain at the 5 km extent was nearly perfectly correlated with the amount of forest measured with the 250 m grain at the 10 km extent ($r=0.95$, $p<0.001$). The amount of forest measured with the 30 m grain was strongly correlated at the 250 m and 1 km extents ($r=0.72$, $p<0.0001$).

3.3.2 Ordinations of bird species and landscape variables

An ordination biplot of bird species and significant landscape variables showed that variable types were somewhat mixed among bird species, but were generally in close proximity in ordination space (Figure 5). Strong associations with the amount of forest at the 4 m grain/90 m extent were evident for great-crested flycatcher, veery and ovenbird, while grey catbird and eastern towhee were associated with the number of forest patches at the 250 m grain/5 km extent. In general, species strongly associated with forest (e.g. red-eyed vireo, eastern wood pewee) and forest-edge species (e.g. black-capped chickadee and American goldfinch) were most closely associated with the explanatory variables used in this analysis. Open-habitat species such as savannah sparrow and bobolink were not positively associated with any of the explanatory variables.

Table 6. Pearson correlation coefficient. Explanatory variables are named [variable type]_[scale] = amount of forest and cv = NDVI variability, and [scale] codes are defined as 250 m, 1 km, 5 km and 10 km extents, respectively.

	mn_i250	cv_i250	fs_1k	fp_15k	mn_11k	mn_15k
mn_i250	1.00	-0.714 <.0001	0.17	-0.02 0.85	0.28 0.01	0.03 0.79
cv_i250	-0.71 <.0001	1.00	0.19 0.07	-0.33 0.00	-0.53 <.0001	-0.34 0.00
fs_i90	0.48 <.0001	-0.057 0.3001	0.001	-0.57 <.0001	-0.05 0.61	-0.55 <.0001
fp_i250	-0.30 0.00	0.032 0.600	0.00	0.34 0.00	0.05 0.66	0.36 0.00
lc_i250	-0.35 0.00	0.527 <.0001	0.01	-0.40 <.0001	-0.38 0.00	-0.37 0.00
fs_l250	0.14 0.19	-0.233 0.000	0.00	-0.40 <.0001	0.25 0.01	-0.35 0.00
lc_l250	-0.18 0.08	0.337 0.000	0.00	-0.26 0.01	-0.24 0.02	-0.37 0.00
fp_l90	0.18 0.09	-0.034 0.900	0.00	-0.29 0.00	0.13 0.21	-0.31 0.00
fp_l250	0.11 0.27	0.133 0.100	0.00	-0.12 0.24	-0.10 0.31	-0.17 0.10
mn_l90	0.42 <.0001	-0.422 <.0003	0.03	-0.22 0.03	0.22 0.03	-0.23 0.02
cv_l90	-0.23 0.02	0.211 0.030	0.00	0.01 0.91	-0.30 0.00	-0.12 0.26
fs_m10k	0.15 0.15	-0.365 0.0001	0.001	0.71 <.0001	0.50 <.0001	0.95 <.0001
fp_m5k	-0.50 <.0001	0.006 0.759	0.00	0.09 0.37	-0.04 0.68	-0.04 0.69
cv_v5k	0.15 0.14	0.152 0.0001	0.001	-0.64 <.0001	-0.27 0.01	-0.83 <.0001
cv_v10k	0.11 0.29	0.125 0.201	0.01	-0.51 <.0001	-0.33 0.00	-0.65 <.0001
fs_l1k	0.20 0.05	-0.228 0.001	0.00	-0.38 0.00	0.53 <.0001	-0.20 0.05
lc_m1k	0.14 0.17	0.100 0.000	0.00	-0.61 <.0001	-0.36 0.00	-0.74 <.0001
fp_l5k	-0.02 0.85	-0.361 0.0001	0.001	1.00	0.29 0.00	0.77 <.0001
mn_l1k	0.28 0.01	-0.436 <.0000	0.00	0.29 0.00	1.00	0.52 <.0001
mn_l5k	0.03 0.79	-0.174 0.0001	0.001	0.77 <.0001	0.52 <.0001	1.00

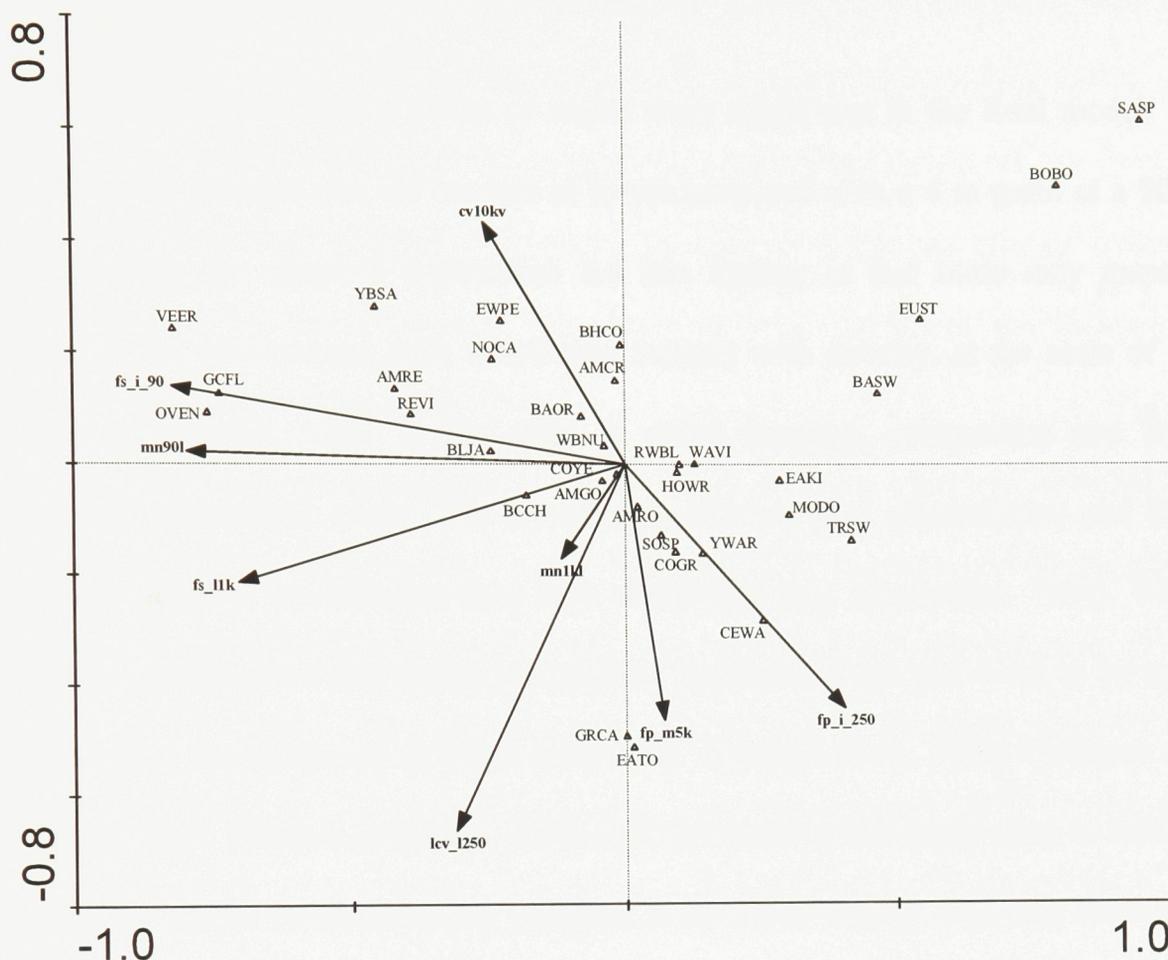


Figure 5. Ordination plot of the first two axes of bird species (triangles) and explanatory variable (arrows) CCA scores. Position of species in relation to arrows indicate relative influence of variable. Only significant ($P < 0.05$) explanatory variables are shown. Bird species acronyms are listed in Table 2. Explanatory variable acronyms are as follows: fs=forest amount, fp=number of forest patches, mn= mean NDVI, cv = coefficient of variation of NDVI, lcv= number of land cover types; i, l, m, and v = 4 m, 30 m, 250 m and 1 km variable grains, respectively, and 90, 250, 1 k, 5k, 10k = 90 m, 250 m, 1 km, 5 km and 10 km variable extents, respectively.

3.4 Discussion

While variables from a range of scales were significant in the final model, the most important variable was the amount of forest measured with a 4 m grain at a 90 m extent. Perhaps the simplest explanation for this finding is that birds may respond strongest to the environment with which they interact with directly, at the scale of the nest site or territory, which is the scale at which foraging, competition and other interspecific interactions occur. The relationship between bird communities and fine-scale environmental variation has long been established (e.g. MacArthur, 1954). While multi-scale studies often find forest composition measured at the plot-level to be more important than that measured at larger scales (e.g. Lichstein et al., 2002; Cushman and McGarigal, 2004; Fletcher and Hutto, 2008) and the results of this study seem to indicate the same, the shared variation among variables at all scales was not explicitly measured. Although the variation partitioning conducted in Chapter 2 indicated that there were differences between the amount of unique variation explained by finer grains, a complete partitioning of variation among grains and extents may reveal important differences between fine and coarse grain and extents. However, because three-quarters of the highest ranked variables in this analysis were fine grain (4 m or 30 m), the importance of microhabitat variables seems quite likely.

In this study, forest amount, a measure of landscape composition, explained more of the total variation in the bird species community than any other variable type by far, including the number of forest patches. While studies generally point to the dominance of composition over configuration (Fahrig, 2003), this study did not explicitly control for the relationship between the amount of forest and the number of forest patches. Given

that a decrease in the amount of forest may increase the number of patches at first until forest amounts are severely reduced and only a few patches remain (Fahrig, 2003), it is difficult to separate the effects of fragmentation from habitat loss. However, the variance explained by the amount of forest compared to the number of patches strongly indicates that composition was more important than configuration in explaining the variation in bird community composition in this study.

Habitat heterogeneity (measured as number of land cover types) was a significant variable in this study when measured at the 30 m grain/250 m extent. NDVI variability was important in explaining bird community composition at the coarsest scale (1 km grain and 10 km extent). The smallest patches (3 ha) used by Freemark and Merriam (1986) are similar to the 250 m extent, and they found that greater habitat heterogeneity increased the number of species and pairs of birds. While Fraser (1998) found the NDVI variability was significantly correlated with species richness using a coarser (10 km) grain than used in this study, and at much larger extents, he did not examine grains as small as 1 km. In this study, species associations were also similar to that in Freemark and Merriam (1986), who found measures of within-forest habitat heterogeneity most important to species such as eastern kingbird, cedar waxwing, mourning dove and American robin.

3.4.1 Conservation recommendations/Limitations

Since the results of the grain and extent analysis in Chapter 2 showed that variation explained across the grains and extents examined was relatively similar, it is not surprising that variables from all grains and extents were significant in the final model. Because species respond to environmental variation at different scales differently,

depending on their grain of perception (Wiens 1989a), a community-level analysis might be expected to find multiple variables important at multiple scales, because each is important to subsets of species (Cushman and McGarigal, 2004). Further, the amount of variation explained in the final CCA model (0.48) is quite high compared to that explained by the individual grains and extents in Chapter 2. Thus, a potentially important implication for bird community research and conservation is that multiscale models that incorporate more than a single type of grain and/or extent may give better results than using only one type of imagery at a fixed extent. Similar results have been found for single-species models, such as those created for the marbled murrelet by Meyer (2007).

4 RESEARCH SUMMARY AND CONCLUSIONS

4.1 *Limitations*

The potential impacts of spatial autocorrelation in the response data and correlation among explanatory variables on the results of the analyses have previously been discussed in this the thesis. Additionally, it is important to acknowledge that land cover maps have many sources of error (Cihlar, 2000). This study used land cover products to derive the majority of the variables, except for NDVI and the IKONOS variables (which may also be susceptible to errors because the clustered product was not validated). Land cover maps result from many interpreter decisions, and there can be significant variability among interpreters (McGwire, 1992). Wickham et al. (1997) demonstrated that classification errors can have a profound impact on landscape metrics.

4.2 *Recommendations for future research*

Although community-level analyses can be both useful and necessary because there may not be enough data for individual species models, additional analyses by functional guilds (such as foraging or migratory strategy) or body size may reveal important species-environment relationships that are scale-dependent that may be more useful from a management perspective. For example, Dunford and Freemark (2004) found that urban and agricultural land uses affected species differently depending on migratory strategy and habitat association, and at different spatial scales. It would also be interesting to see if similar results are obtained using individual logistic regression models of bird species, especially for the grain and extent study in Chapter 2. Since species respond to the environment at different scales individually, including all species in a community- level analysis may be averaging out the response across all species.

Perhaps most importantly, future work should test for, and if necessary, incorporate spatial autocorrelation in the response variable into models to further clarify the roles that environmental variables play at different spatial scales. To test whether species/environmental variables are correlated by scale, Mantel correlograms, a specialized version of the Mantel test that subsets the autocorrelation into discrete distance classes, can be used to explicitly consider the spatial structure of multivariate data (Legendre and Fortin, 1989; e.g. King et al., 2004). Dormann et al. (2007) review the methods available to correct parameter estimates including spatial eigenvector mapping (suitable for community level data) as well as autocovariate models and spatial models based on generalized least squares regression. An additional possibility is a novel method that allows CCA to be partitioned by distance and integrated with geostatistics, described by Wagner (2004).

Finally, this study examined only the most commonly used explanatory variables that can be derived from satellite remote sensing land cover and reflectance data. Other studies have used different or more sophisticated approaches to quantify bird-habitat relationships at multiple scales. For example, St. Louis et al. (2006) found image texture measures such as the standard deviation of pixel values (a measure of spectral variability and habitat heterogeneity) from orthophotos was a good predictor of species richness at a number of different scales. Other studies, such as Clawges et al. (2008) have used lidar, a high resolution sensor that can measure 3-dimensional vegetation structure to quantify habitat important to birds. Once general patterns have been established using easily derived metrics like the ones used in this thesis, repeating the analyses with a more

sophisticated suite of remote sensing measures may provide further insights into the mechanisms driving patterns of species distributions at different scales.

4.3 Conclusions

The research in Chapter 2 found only small differences in the amount of variation in the bird data that could be independently explained by each grain and extent, within the groups examined. The research in Chapter 3 found that fully three-quarters of the significant variables were finer grain, supporting the idea that variables measured at fine grains likely capture information on some important aspects of microhabitat not discernable by other grains. While the most important variable by far was the amount of forest at the finest scale, each variable type and scale was represented in the final model, likely due to the differences in the individual species' responses to environmental heterogeneity. Multiscale studies that systematically vary the grain and extent of the explanatory variables, covering a more complete range of the environmental gradient over a larger geographical extent are needed before generalizations can be made about the independent contributions of variable grain and extent, and in order to better elucidate the mechanisms determining bird distribution at different scales.

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Appendix A. Modified FGDC land cover legend used for the Landsat, MODIS and VGT land cover products used in this thesis.

Tree Dominated (tree crown density > 25%)	
1	Evergreen forest (>75% cover) – old
3	Deciduous forest (>75% cover)
4	Mixed coniferous (50-75% coniferous) – old
5	Mixed coniferous (50-75% coniferous) – young
6	Mixed deciduous (25-50% coniferous)
7	Evergreen open canopy (40-60% cover) - moss-shrub understory
8	Evergreen open canopy (40-60% cover) - lichen-shrub understory
9	Evergreen open canopy (25-40% cover) - shrub-moss understory
10	Evergreen open canopy (25-40% cover) - lichen (rock) understory
11	Deciduous open canopy (25-60% cover)
13	Mixed evergreen-deciduous open canopy (25-60% cover)
14	Mixed deciduous (25-50% coniferous trees; 25-60% cover)
Shrub Dominated	
16	Deciduous shrubland (>75% cover)
Herb Dominated	
18	Herb-shrub-bare cover, mostly after perturbations
20	Wetlands
22	Sparse coniferous (density 10-25%), herb-shrub cover
23	Herb-shrub
28	Low vegetation cover (bare soil, rock outcrop)
30	Woodland-cropland
31	Cropland-woodland
32	Annual row-crop forbs and grasses - high biomass
33	Annual row-crop forbs and grasses - medium biomass
34	Annual row-crop forbs and grasses - low biomass
Vegetation Not Dominant	
38	Rock outcrop, low vegetation cover
39	Recent burns
40	Mostly bare disturbed areas (e. g. cutovers)
41	Low vegetation cover
42	Urban and built-up
43	Water bodies

Appendix B. Arc/INFO Log file of key GRID processing steps used to create explanatory variables from satellite imagery.

*/ number of land cover types

```

200703261551  1   17   0aclousto LC_VAR_L_90 = focalvariety(landsat_lc, rectangle, 3,
3, data)
200703261554  1   65   0aclousto LC_VAR_L_250 = focalvariety(landsat_lc, rectangle,
8, 8, data)
200703261622  14   11   0aclousto LC_VAR_I_90 = focalvariety(ikonos_lc, rectangle, 22,
22, data)
200703261633  0    1   0aclousto LC_VAR_M_1K = focalvariety(modis_lc, rectangle, 4,
4, data)
200703261730  18  199   0aclousto LC_VAR_L_1K = focalvariety(landsat_lc, rectangle,
33, 33, data)
20070327 158 508 -137   0aclousto LC_VAR_L_5K = focalvariety(landsat_lc, rectangle,
167, 167, data)
20070327 406 128  343   0aclousto LC_VAR_I_250 = focalvariety(ikonos_lc, rectangle,
62, 62, data)
20070327 406  0    9   0aclousto LC_VAR_M_5K = focalvariety(modis_lc, rectangle, 20,
20, data)
20070327 407  1 -392   0aclousto LC_VAR_M_10K = focalvariety(modis_lc, rectangle, 40,
40, data)
20070327 407  0    0   0aclousto LC_VAR_V_5K = focalvariety(vgt_lc, rectangle, 5, 5,
data)
20070327 407  0    1   0aclousto LC_VAR_V_10K = focalvariety(vgt_lc, rectangle, 10,
10, data)

```

*/ number of forest patches

```

200703271706  0    0   0aclousto FORPAT_V = regiongroup(fornon_v, #, four, #, 0)
200703271709  0    0   0aclousto FORPAT_V_5K = focalvariety(forpat_v, rectangle, 5,
5, data)
200703281342  0    0   0aclousto FORPAT_V_10K = focalvariety(forpat_v, rectangle, 10,
10, data)
200703271729  0   13   0aclousto FORPAT_L = regiongroup(fornon_l, #, four, #, 0)
200703271729  0    0   0aclousto FORPAT_M = regiongroup(fornon_m, #, four, #, 0)
200703271729  0   13   0aclousto FORPAT_L_90 = focalvariety(forpat_l, rectangle, 3,
3, data)
200703271730  1   53   0aclousto FORPAT_L_250 = focalvariety(forpat_l, rectangle, 8,
8, data)
200703271744  14  -49   0aclousto FORPAT_L_1K = focalvariety(forpat_l, rectangle, 33,
33, data)
200704101620  0    1   0aclousto FORPAT_M = regiongroup(fornon_m, #, four, #, 0)
200704101623  0    0   0aclousto FORPAT_M_1K = focalvariety(forpat_m, rectangle, 4,
4, data)
200704101623  0    6   0aclousto FORPAT_M_5K = focalvariety(forpat_m, rectangle, 20,
20, data)
200704101624  1 -401   0aclousto FORPAT_M_10K = focalvariety(forpat_m, rectangle, 40,
40, data)
200703291734  0   20   0aclousto FORPAT_I = regiongroup(fornon_i, #, four, #, 0)
200703291746  10  146   0aclousto FORPAT_I_90 = focalvariety(forpat_i, rectangle, 22,
22, data)
20070407 534 738  40   0aclousto FORPAT_I_250 = focalvariety(forpat_i, rectangle, 62,
62, data)

```

*/ NDVI

```

200703301452  0   18   0aclousto NDVI_I = int(((i_nir_fl - i_red_fl) / (i_nir_fl +
i_red_fl)) * 100)
200703301453  0    0   0aclousto M_NIR_FL = float(modis_nir)
200703301453  0    0   0aclousto M_RED_FL = float(modis_red)
200703301455  0    0   0aclousto NDVI_M = int(((m_nir_fl - m_red_fl) / (m_nir_fl +
m_red_fl)) * 100)
200703301456  0    5   0aclousto V_RED_FL = float(vgtred)
200703301456  0    5   0aclousto V_NIR_FL = float(vgtnir)

```

```

200703301457  0      8      0aclousto NDVI_V = int(((v_nir_fl - v_red_fl) / (v_nir_fl +
v_red_fl)) * 100)

*/ NDVI Variability

200703301610  9     110    0aclousto I_SD_90 = focalstd(ndvi_i, rectangle, 22, 22, data)
200703301719  69   -171    0aclousto I_SD_250 = focalstd(ndvi_i, rectangle, 62, 62, data)
200703301720  1     15     0aclousto L_SD_90 = focalstd(ndvi_l, rectangle, 3, 3, data)
200703301720  0     57     0aclousto L_SD_250 = focalstd(ndvi_l, rectangle, 8, 8, data)
200703301734  14    -41     0aclousto L_SD_1K = focalstd(ndvi_l, rectangle, 33, 33, data)
200703302335  361   108    0aclousto L_SD_5K = focalstd(ndvi_l, rectangle, 167, 167,
data)
200703302335  0     1     0aclousto M_SD_1K = focalstd(ndvi_m, rectangle, 4, 4, data)
200703302335  0     6     0aclousto M_SD_5K = focalstd(ndvi_m, rectangle, 20, 20, data)
200703302336  1    24     0aclousto M_SD_10K = focalstd(ndvi_m, rectangle, 40, 40, data)
200703302336  0    20     0aclousto V_SD_5K = focalstd(ndvi_v, rectangle, 5, 5, data)
200703302337  1    57     0aclousto V_SD_10K = focalstd(ndvi_v, rectangle, 10, 10, data)
200703302344  7    25     0aclousto I_MN_90 = focalmean(ndvi_i, rectangle, 22, 22, data)
20070331  42   58     27    0aclousto I_MN_250 = focalmean(ndvi_i, rectangle, 62, 62,
data)
20070331  42   0     12    0aclousto L_MN_90 = focalmean(ndvi_l, rectangle, 3, 3, data)
20070331  43   1     44    0aclousto L_MN_250 = focalmean(ndvi_l, rectangle, 8, 8, data)
20070331  54  11   -247   0aclousto L_MN_1K = focalmean(ndvi_l, rectangle, 33, 33, data)
20070331  528 274   74    0aclousto L_MN_5K = focalmean(ndvi_l, rectangle, 167, 167,
data)
20070331  528 0     0     0aclousto M_MN_1K = focalmean(ndvi_m, rectangle, 4, 4, data)
20070331  528 0     5     0aclousto M_MN_5K = focalmean(ndvi_m, rectangle, 20, 20, data)
20070331  528 0    18    0aclousto M_MN_10K = focalmean(ndvi_m, rectangle, 40, 40,
data)
20070331  528 0    19    0aclousto V_MN_5K = focalmean(ndvi_v, rectangle, 5, 5, data)
20070331  529 1    51    0aclousto V_MN_10K = focalmean(ndvi_v, rectangle, 10, 10,
data)

*/ amount of forest

200704051714  0     16    0aclousto FORSUM_L_90 = focalsum(fornon_l, rectangle, 3, 3,
data)
200704071018  284  241    0aclousto FORSUM_I_90 = focalsum(fornon_i, rectangle, 22, 22,
data)
2007040822212163  -1    0aclousto FORSUM_I_250 = focalsum(fornon_i, rectangle, 62, 62,
data)
200704082222  1     60    0aclousto FORSUM_L_250 = focalsum(fornon_l, rectangle, 8, 8,
data)
200704082236  14   -45    0aclousto FORSUM_L_1K = focalsum(fornon_l, rectangle, 33, 33,
data)
20070409  443 367   57    0aclousto FORSUM_L_5K = focalsum(fornon_l, rectangle, 167,
167, data)
20070409  443 0     0     0aclousto FORSUM_M_1K = focalsum(fornon_m, rectangle, 4, 4,
data)
20070409  443 0     5     0aclousto FORSUM_M_5K = focalsum(fornon_m, rectangle, 20, 20,
data)
20070409  443 0    18    0aclousto FORSUM_M_10K = focalsum(fornon_m, rectangle, 40, 40,
data)
20070409  443 0     1     0aclousto FORSUM_V_5K = focalsum(fornon_v, rectangle, 5, 5,
data)
20070409  443 0     0     0aclousto FORSUM_V_10K = focalsum(fornon_v, rectangle, 10, 10,
data)

```

Appendix C. Summary statistics for the 55 explanatory variables sampled at the 95 bird survey locations. Variables follow the naming convention [variable_grain_extent], where the variable CV = NDVI variability, FP = the number of forest patches, FS = the amount of forest, LC = the number of land cover types and MN = mean NDVI; the grains i, l, m, and v = 4 m, 30 m, 250 m and 1 km grains, respectively, and the extents 90, 250, 1 k, 5k, 10k = 90 m, 250 m, 1 km, 5 km and 10 km extents, respectively. *Mean, minimum and maximum of forest amount have been standardized to hectares, to facilitate comparison of different grains.

Variable	Mean	Coefficient of Variation	Minimum	Maximum
cv_i_250	27.16	56.20	7.00	96.00
cv_i_90	25.66	44.30	7.00	72.00
cv_l_1k	150.78	237.29	16.00	2631.00
cv_l_250	72.24	335.46	6.00	2142.00
cv_l_5k	1178.00	400.68	30.00	44917.00
cv_l_90	26.18	158.20	3.00	373.00
cv_m_10k	787.96	182.24	27.00	10597.00
cv_m_1k	386.54	563.98	4.00	21015.00
cv_m_5k	675.93	206.38	11.00	11094.00
cv_v_10k	7.84	25.99	3.00	11.00
cv_v_5k	7.32	54.32	1.00	14.00
fp_i_250	64.98	58.12	2.00	169.00
fp_i_90	11.09	60.98	1.00	28.00
fp_l_1k	13.00	46.21	3.00	30.00
fp_l_250	2.87	44.61	1.00	7.00
fp_l_5k	185.66	31.69	78.00	313.00
fp_l_90	1.55	44.98	1.00	4.00
fp_m_10k	32.54	35.86	11.00	58.00
fp_m_1k	2.34	28.34	1.00	4.00
fp_m_5k	10.57	43.70	2.00	18.00
fp_v_10k	2.40	28.77	2.00	5.00
fp_v_5k	2.04	17.37	1.00	3.00
*fs_i_250	2.52	61.60	0.0016	5.82
*fs_i_90	0.29	71.67	0.00	0.77
*fs_l_1k	36.95	54.95	1.80	82.80
*fs_l_250	1.89	84.92	0.00	5.76
*fs_l_5k	849.78	26.88	280.89	1350.90
*fs_l_90	0.16	143.94	0.00	0.81
*fs_m_10k	4105.25	19.97	2862.50	5787.50
*fs_m_1k	50.56	50.52	6.25	100.16
*fs_m_5k	1215.25	18.59	700.00	1850.00
*fs_v_10k	3561.00	45.47	1500.00	7600.00
*fs_v_5k	1115.00	63.23	100.00	2500.00
lc_i_250	25.93	17.32	13.00	38.00
lc_i_90	20.60	21.97	7.00	30.00
lc_l_1k	8.38	11.31	6.00	9.00

lc_l_250	5.16	29.70	2.00	8.00
lc_l_5k	9.21	4.45	9.00	10.00
lc_l_90	2.69	34.69	1.00	6.00
lc_m_10k	21.98	12.42	17.00	28.00
lc_m_1k	4.56	45.79	2.00	10.00
lc_m_5k	14.88	23.39	6.00	20.00
lc_v_10k	3.77	11.90	3.00	5.00
lc_v_5k	2.91	24.63	1.00	4.00
mn_i_250	4844.00	18.29	2369.00	6497.00
mn_i_90	4812.00	18.87	2796.00	6566.00
mn_l_1k	2826.00	35.77	117.00	4352.00
mn_l_250	3288.00	30.44	134.00	4823.00
mn_l_5k	1731.00	75.33	8.00	3870.00
mn_l_90	3298.00	31.17	255.00	5266.00
mn_m_10k	1346.00	56.58	42.00	3143.00
mn_m_1k	2267.00	44.11	18.00	4843.00
mn_m_5k	1816.00	61.40	37.00	3416.00
mn_v_10k	7566.00	3.03	6953.00	7957.00
mn_v_5k	7436.00	5.43	6159.00	8055.00

Appendix D. Results of Chapter 3 initial forward selection procedure, grouped by the 5 explanatory variables. The twenty significant variables ($P < 0.05$) retained for the final CCA model are indicated with an asterisk (*). Variable codes are provided in Appendix C.

Variable	Variance Explained	P	F
mn_l_90	0.14	0.001*	5.88
mn_l_5k	0.06	0.001*	2.83
mn_l_1k	0.05	0.001*	2.3
mn_i_250	0.05	0.001*	2.13
mn_m_10k	0.03	0.093	1.36
mn_v_10k	0.03	0.23	1.18
mn_m_1k	0.02	0.307	1.12
mv_v_5k	0.03	0.293	1.13
mn_l_250	0.02	0.435	1.01
mn_m_5k	0.02	0.457	1
mn_i_90	0.02	0.523	0.97
lc_m_1k	0.08	0.001*	3.26
lc_l_250	0.05	0.002*	2.43
lc_i_250	0.05	0.01*	1.87
lc_v_5k	0.03	0.103	1.37
lc_l_90	0.03	0.149	1.26
lc_v_10k	0.03	0.266	1.13
lc_l_5k	0.02	0.355	1.07
lc_i_90	0.03	0.296	1.12
lc_l_1k	0.02	0.462	1
lc_m_5k	0.02	0.759	0.8
lc_m_10k	0.02	0.582	0.92
cv_v_5k	0.07	0.001*	3.01
cv_l_90	0.07	0.001*	2.69
cv_v_10k	0.04	0.001*	2.11
cv_i_250	0.04	0.02*	1.68
cv_m_1k	0.03	0.118	1.34
cv_m_5k	0.03	0.168	1.25
cv_i_90	0.03	0.154	1.29
cv_l_5k	0.03	0.23	1.22
cv_m_10k	0.03	0.333	1.13
cv_l_1k	0.02	0.51	0.98
cv_l_250	0.02	0.737	0.79

Variable	Variance Explained	P	F
fs_i_90	0.14	0.001*	6.13
fs_l_1k	0.07	0.001*	3.11
fs_m_10k	0.04	0.005*	1.83
fs_l_250	0.04	0.048*	1.48
fs_i_250	0.03	0.068	1.43
fs_v_10k	0.03	0.174	1.25
fs_m_5k	0.02	0.196	1.21
fs_m_1k	0.03	0.256	1.15
fs_v_5k	0.02	0.377	1.06
fs_l_90	0.02	0.636	0.88
fs_l_5k	0.02	0.968	0.6
fp_l_90	0.08	0.001*	3.22
fp_l_5k	0.05	0.004*	2.08
fp_l_250	0.04	0.009*	1.87
fp_m5k	0.04	0.007*	1.88
fp_i_250	0.05	0.007*	1.9
fp_v_5k	0.02	0.216	1.2
fp_v_10k	0.03	0.236	1.15
fp_m_10k	0.03	0.363	1.07
fp_l_1k	0.02	0.388	1.06
fp_i_90	0.02	0.488	0.98
fp_m_1k	0.02	0.761	0.79