

**Modelling Native Bird Diversity
in the Greater Toronto Area**

by

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A thesis

presented to the University of Waterloo

in fulfillment of the

thesis requirement for the degree of

Master of Environmental Studies

in

Environment and Resource Studies

Waterloo, Ontario, Canada, 2005

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Author's declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Abstract

Human-dominated landscapes often have habitat loss and fragmentation. These characteristics described at the landscape scale, called landscape elements, influence species diversity and distribution. These landscape elements include such descriptions as the amount of habitat in the landscape and the degree of fragmentation of the habitat. "Optimization of landscape pattern" studies which landscape elements will maximize species diversity and/or distribution. Some general conclusions have emerged from this research. For example, for some bird species the size of the habitat patch in which a species nests has been found to be more important than landscape variables. However, preliminary research suggested that landscape elements such as the matrix are important urban areas. My study addressed this problem by asking: which elements of the landscape are most important for predicting avian species richness and abundance in the Greater Toronto Area? A literature review revealed a number of variables that have been found to influence bird species diversity within a landscape: area of habitat in which the species nests, amount of habitat within the landscape, degree of fragmentation, vegetation characteristics of the habitat patch, and area within the landscape deemed urban in municipal land-use designations (amount of urbanization). From this literature, I formulated four hypotheses describing the most important variables for avian diversity: (1) the area of the habitat patch is most important, (2) only variables describing the habitat patch itself are important, (3) the area of the habitat patch is important, but landscape variables should also be considered and (4) urbanization is most important. These hypotheses were considered competing explanations of bird species diversity at the landscape scale.

A database of breeding bird data and landscape information, in a geographic information system platform, was used to investigate the comparative strength of the competing hypotheses for the Greater Toronto Area. A mathematical expression with a Poisson model format was created to represent each hypothesis. The model selection technique based on Kullback-Leibler information using the Akaike Information Criterion was deemed most appropriate for the comparison of the models. Four separate Poisson model competitions were completed using two habitat types and two response variables: species richness and total abundance. In three of the four competitions, the best model included the habitat area and the amount of urbanization in the landscape. In the fourth competition, this model was considered as strong as another model which included habitat area, amount of habitat in the landscape and degree of fragmentation. The results from the model competition support the hypothesis that habitat area is important, but landscape variables must also be considered to explain avian richness and total abundance. It appears that maintaining native bird biodiversity in the Greater Toronto Area should focus on preserving and possibly increasing habitat area and decreasing adjacent urbanization. Exploration of the best model in the forest analysis with the richness response variable found that a 10% increase in habitat area cause approximately a 10% increase in species richness, and a 10% increase in urban

area caused approximately a 20% decrease in species richness. Consequently, current natural heritage planning in Ontario should consider urban development as an important negative effect on native birds.

Acknowledgements

This project would not have happened without the generous supply of data from the Toronto and Region Conservation Authority. The richness of data available for this project was only possible through the dedicated planning and field work of the knowledgeable staff at TRCA. I am especially grateful to Dan Clayton and Patricia Moleirinho who assisted with data requests. Natalie Iwanyki, Paul Prior, Lionel Normand and Sue Hayes answered my technical questions and provided significant support.

The execution and conclusion of my project was possible through the assistance of my supervisor, Dr. Stephen Murphy, who provided consistent guidance and support. His critiques and comments improved this project, and his reassurance and sense of humour were invaluable. Dr. Thomas Nudds also provided considerable guidance. I am especially appreciative of his assistance with the methodology for my project. His enthusiasm and sense of humour inspired my continued work towards the project's completion.

Judith Toms and other statisticians at the University of Waterloo, including Dr. R. Jeanette O'Hara Hines, were instrumental in both the planning and analysis of my project. Their time and effort is much appreciated.

The computer assistance through Environmental Studies at the University of Waterloo was extremely important. Scott MacFarlane provided invaluable assistance with the GIS programming. He saved me considerable frustration with this aspect of my project. My friends and colleagues at the University of Waterloo provided wonderful inspiration and an excellent social reprise. I learned a lot beyond this single project from their varied experiences, insightful thoughts and discussions. Thanks as well to the faculty of Environment and Resource Studies at the University of Waterloo. What an inspirational and dedicated group of people!

Last, but not least, I would like to thank my never-failing family. Thanks especially to my partner Kenneth Moore who has provided consistent support. He has also been an intelligent and insightful sounding-board for my ideas and frustrations. Thanks as well to my grandparents, Anne Cummings and Theodore Hallberg, who have always been there for my pursuits of knowledge. They have been my inspiration for my academic and personal achievements. Thanks to my mother Rhonda Hallberg who is always there to help and an inspiration for hard work and dedication. Thanks to my father Carl Zajc who always supports all my scholastic and employment ventures.

Thanks as well to all my friends living further a field. Their love and support is always greatly appreciated. Thanks especially to Stephanie Côté, Shannon Stephens and Jolene Smith.

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1.0 Introduction

In Canada, approximately eighty percent of the population lives in urban areas, and many of Canada's larger urban centers, such as Toronto, are expected to experience population growth (Sahley et al. 2003). In exurban areas, where much development occurs, habitat may still be present. There is concern that urbanization surrounding this habitat may have a detrimental effect for resident species. Certain species of birds have been identified as particularly vulnerable to fragmentation, habitat loss and urbanization. Friesen et al. (1995) showed, for example, that area effects were magnified in habitats surrounded by high-density residential development relative to low-density development. This concern for bird populations has been heightened by observed population declines of some species such as avian neotropical migrants (Ownes & Bennett 2000).

1.1 Optimization of landscape pattern

Landscapes affected by fragmentation and habitat loss are complex; they contain a diversity of habitat and non-habitat in convoluted configurations. It is still unclear the influence such landscape factors as habitat loss, fragmentation or other disturbances may have on species residing in these complex landscapes. The landscape ecology discipline assumes that landscape pattern influences the flow of materials and energy (Wu & Hobbs 2002). Following this assumption, a current pursuit in landscape ecology aims to untangle the influence and relative importance of the different landscape elements to species diversity and persistence (Andr n 1994; Cushman & McGarigal 2004; Fahrig 1997; Guerry & Hunter 2002), as well as the relative importance of spatial scale (Berry & Bock 1998; Burke & Nol 2000; Crozier & Niemi 2003; Cushman & McGarigal 2002). Wu and Hobbs (2002) termed these studies of "optimization of landscape pattern". This research area investigates if and how landscape pattern can be optimized in both composition and configuration of habitat and the matrix for the purpose of species conservation (Wu & Hobbs 2002). My specific type of optimization of landscape pattern study investigates which landscape elements appear to be most strongly related to species diversity.

Landscape elements are here defined as the structural characteristics of the landscape including the amount of habitat in the landscape, degree of fragmentation of that habitat and the characteristics of the matrix, all of which create the landscape pattern of habitat and non-habitat (Forman & Godron 1986).

Some general conclusions have emerged from this literature, such as the assertion that habitat size may be more important than attributes of the surrounding landscape (e.g. Cushman & McGarigal 2004). Results from a few studies that considered urbanization suggest that some of these relationships found for studies of optimization of landscape pattern may not hold for urban landscapes. For example, Friesen et al. (1995) found that residential development had a

significantly negative effect on neotropical migrant birds independent of size class of forests. This suggests that adjacent land-use may have an important effect on bird populations, and perhaps this effect is greater in urban areas than in non-urban areas. It appears that landscape ecology studies should investigate which landscape elements are most important in urban areas.

1.2 Study purpose and research question

My research can be considered a study of optimization of landscape pattern. I am interested in which characteristics of the habitat and/or matrix in the landscape is most important for predicting avifauna diversity. Few studies have researched the optimization of landscape pattern for species conservation while considering urban development as a factor in the landscape. My study focuses on native avifauna in the Greater Toronto Area. The research question asks: which elements of the landscape are most important for predicting avian species richness and abundance in the Greater Toronto Area?

Model competition was used to determine the most important landscape and habitat variables for avian richness and abundance. This technique is based on Kullback-Leibler information, and it uses the Akaike Information Criterion as an unbiased, robust estimator of the explanatory strength of a statistical model for a given set of data (Burnham & Anderson 1998). Various hypotheses describing the most important variables in the landscape to explain avian diversity were generated from the literature. Models used to represent these hypotheses were then compared in terms of their explanation of the data.

Birds have been chosen because, as a diverse group with different natural histories and biological strategies, they present a variety of responses to the landscape (Odell & Knight 2001). Also, birds have also been studied extensively (Germaine et al. 1998), so there is generally good understanding in the literature of their natural histories. This wealth of information can inform later exploration of possible cause and effect relationships. Furthermore, as illustrated in the following sections, it has been shown that birds likely respond to attributes of both the habitat patch and the surrounding landscape, including urbanization. Consequently, they are ideal for exploring the optimization of landscape pattern.

The Greater Toronto Area was chosen because it is a rapidly developing urban centre, and it has a rich database of landscape and species information, so hypotheses could be tested. Such data is lacking for most comparable centers. These data form the quantitative basis of my project.

1.3 Gaps in current policy in Ontario

Determining the most important landscape elements for species diversity, especially within the urban context, has implications for environmental management and planning (Fraser 2003). This understanding can focus planning, management and restoration activities to these particular landscape features. For example, if habitat area is the only important variable for species biodiversity, then policies, such as the policy for the protection of natural features in Ontario (Ministry of Municipal Affairs and Housing 1997), should focus on habitat characteristics more than adjacent land-use. Current policies in Ontario are vague as to the most important ways in which biodiversity can be planned and managed in the urbanizing landscape of the Greater Toronto Area. Studies such as this one can identify and focus actions for species conservation. Without an informed understanding of which landscape elements may be most important, resources allocated for conservation may be directed towards action that has little effect on the desired outcome of species conservation.

1.4 Definitions

This study relies upon many concepts that are variously defined in the literature and in popular use. For clarification, I will define the specific terms that are relevant. Although biodiversity can be conceptualized at different temporal and spatial scales or for different biological units (e.g. genes or species), for this study, biodiversity is considered at the species scale with particular focus on avifauna. Biodiversity will be quantified as total species abundance (the total number of individuals per habitat patch) and species richness (the total number of different species per habitat patch).

Landscape ecology provides an approach for considering coarser spatial scales. It is a branch of ecology concerned with heterogeneity in space and in time (Sanderson & Harris 2000) and species interactions at a broader spatial scale (Bissonette 1997). This study takes the same perspective as authors who regard the landscape as a subjective scale defined by the study organism (Allen 1998). The methods (Section 2) will further elaborate on the specific chosen scale for the landscape. Briefly, the landscape scale in this study is defined as a larger spatial area that is greater than an individual's territory and encompassing the area used for feeding and other daily activities (home-range)(Forman & Godron 1986:361).

My study focuses on both habitat loss and fragmentation. Fragmentation is the breaking apart of habitat. The main components of fragmentation include the loss of original habitat, reduction of habitat patch size and the increased isolation of patches (Andr n 1994). I have followed recommendations from Fahrig (2003) to separate habitat loss from the concept of fragmentation.

In the fragmented landscapes of southern Ontario, there is a complex juxtaposition of remnant habitat areas (of various types and different sizes and shapes) and human-dominated elements that form a matrix in which the habitat is embedded (Larson et al. 1999). In general, the matrix is defined as the most connected element of the landscape (Forman & Godron 1986), and in southern Ontario, the matrix is usually dominated by such human activities as agriculture, industry, or urban development, including a network of transportation corridors. The matrix surrounds the fragmented habitat pieces that are here referred to as habitat patches.

Urban areas are usually distinguished from exurban areas by the greater population density (Statistics Canada 2003). For this study, the urbanization variable was derived from existing database information that was generated from the developed areas identified in current municipal Official Plans (Iwanyki 2004).

1.5 Introduction to Literature Review

Numerous theories, models and hypotheses have been formulated to address the factors explaining diversity and spatial species distribution (Bestelmeyer et al. 2003). Although relatively immature in its theoretical framework (Haines-Young 1999; Wiens 1992), those who work in landscape ecology have proposed predictions of the effects of the elements of the landscape on species (see Melles et al. 2003). Two important theories are the equilibrium theory of island biogeography (e.g. MacArthur & Wilson 1967) and metapopulation theory (e.g. Hanski & Simberloff 1997). These are considered dispersal-based theories; they rely on the action of organism dispersal, particularly the immigration of individuals to sub-populations. Both theories have been applied to complex landscapes that experienced habitat loss, fragmentation and other disturbances (Collinge 1996).

Theoretical development and on-going research in landscape ecology have proposed particular landscape elements that may affect species persistence. Under the umbrella of island biogeography, habitat area and isolation are considered important (MacArthur & Wilson 1967). Distance between habitats (isolation) is also important in metapopulation models, which require movement of organisms between habitat patches for regional population persistence (Andrén 1994). Extension of these two theories considers the intervening matrix (the area in which organisms travel) as a potentially important factor (Rodewald 2003), including the possible effects of different matrix types (Bayne & Hobson 1997; Rodewald & Yahner 2001). Considerations of habitat area have included investigation of the effects of habitat edges. For birds, the edge can have greater rates of predation or parasitism (Askins 1995; Donovan et al. 1997; Patten & Boler 2003) and lower food availability (Burke & Nol 2000), thereby potentially reducing the effective area of the habitat patch for some species (Freemark et al. 1995; Mörtberg 2001).

This literature review explores the landscape variables that potentially affect species. It has three main purposes: to discern the most important variables explaining avian species distribution across different landscape types, to understand the general type of relationship found between these variables and diversity measures, and to identify the gaps in the literature pertaining to landscape pattern effects on avian species distribution and diversity. The methods (Section 2.0) will build on this literature to create competing models to address the research question.

My exploration of the literature has focused on the landscape perspective. Two ways of describing the landscape have been associated with bird diversity and distribution: habitat patch variables, which describe characteristics of the habitat patch in which the species is nesting and landscape variables, which describe the area surrounding the habitat patch (e.g. MacAlpine & Eyre 2002). For both categories, numerous metrics can be formulated. I have limited the number of metrics considered in this literature review; I have focused on a smaller number of well established metrics in order to avoid over-fitting models of species diversity that results from adding a multitude of explanatory variables.

Through exploration of the literature pertaining to these two categories of variables and birds, I have found that two types of metrics are common for habitat patch descriptors: those describing the geometry of the patch and those describing the vegetation of the patch. Of the varied ways to describe the geometry of the patch, habitat patch area is most common, and, as described in the following section, habitat patch area is strongly associated with bird diversity.

Landscape scale variables are commonly categorized as describing landscape composition (the amount and type of habitat in the landscape) and landscape configuration (the spatial pattern of the habitat)(e.g. MacAlpine & Eyre 2002). Here, I have labeled these categories ‘adjacent habitat’ and ‘fragmentation’ measures. I have also considered the characteristics of the intervening matrix as a landscape variable.

1.6 Birds and patch variables

Within the habitat patch, vegetation characteristics such as canopy closure and floristics (vegetation composition) may be important (Askins et al. 1987) for predicting bird species distribution and diversity. For example, Miller et al. (2003) found that local habitat variables explained twice the variation of avian diversity in riparian areas than their landscape variable of settlement intensity. Other researchers have found vegetation measures to be unimportant in relation to area measures in assessing avian diversity (Blake & Karr 1987). It appears that although nest site vegetation characteristics may be well known for many species, no general conclusion has been reached on the relative importance of patch level vegetation characteristics. However,

vegetation is still important for my study because of the relationship between it and other variables such as urbanization (see Section 1.8).

The effect of patch size for birds has been intensely studied in relation to various measures of bird diversity including species richness, abundances and density. A small number of studies investigated the relationship between patch size and breeding success. The specific measure of bird diversity affects the observed relationship with area (Cushman & McGarigal 2002), thus the following review summarizes the findings of each study approach separately.

Studies as early as the 1970s investigated the effect of remnant patch size on bird abundance (Forman et al. 1976). Habitat patch area has been found to be a significant predictor variable for abundance for many species. Crozier and Niemi (2003) found that 12 out of 17 species-specific linear regression models retained area as the only important variable for long-distance migrants. Short distance migrants similarly retained area for 11 out of 18 models. Overall, patch area was a significant variable in 38 of 40 models while other landscape and patch variables were only retained in models for a few species. Individual neotropical migrant species abundance has been strongly associated with area (Austen et al. 2001). Lee et al. (2002) found that they were more consistently associated with habitat area than landscape variables.

Not all studies have found a significant and positive relationship between habitat area and abundance. Subsequent investigations revealed that area has a complex relationship with abundance (Blake & Karr 1987). Crooks (2004) found that area was only marginally related to abundance summed across species, and certain categories of birds had a negative relationship with area. This indicates that patch area could be an important variable for understanding species abundance, but it may not be the only significant variable for certain species.

Research has revealed that area is a strong predictor of bird species richness. Investigation of the literature shows that the species-area relationship can generally be described as a positive logarithmic curve (Ambuel & Temple 1983; Crooks et al. 2004; Freemark & Merriam 1986). This relationship is strongly significant for many groups of species; in a number of studies the area variable described a large portion of the variance in species richness. Blake and Karr (1987) noted that previous studies consistently demonstrated that approximately fifty percent of the variation in species richness was explained by area. Recently, Bellamy and others (1996) summarized that 16-98% of the variation in species richness was explained by area.

Some groups of birds have been found to have a stronger association with area than other groups. Bellamy et al. (1996) found that most of the variation of woodland species richness was explained by area. Freemark and Merriam (1986) categorized birds into a number of different groupings based on life history characteristics and found that 11 of 16 models included area. In general, groupings of species considered more “sensitive” or “specialized”, such as woodland species or long-distance migrants, strongly associate with patch area.

Current research has started to investigate reproductive success in relation to area. This data is only available for a few species. Burke and Nol (2000) executed such a study in Ontario for ovenbirds. They found that reproductive success related to patch area and successful breeding did not occur at woodlot sizes below a threshold. Similarly, Mörtberg (1999) found, through logistic regression models of breeding probability for nuthatches in Sweden, that there was a significant, positive relationship with area and a strong preference for larger woodlots.

Several explanations exist to accompany the demonstration of the positive species-area relationship. This phenomenon has been partially attributed to “edge effects”, particularly in forests (Collinge, 1996). Larger patches become biologically important because they provide a larger area of “interior habitat” that is not edge, and they support species that require interior habitat, which may not be found in smaller patches. Smaller patches can also have a negative effect on the extinction rate of the patch population (Debinski & Holt 2000). These smaller populations may be more vulnerable to extinction due to interspecific interactions, predation or brood parasitism (Collinge 1996). Lastly, larger patches may simply support more diversity due to increased habitat heterogeneity that provides for more species (e.g. Boecklen 1986). An interesting new hypothesis suggests that some bird species may preferentially choose larger patches to increase opportunities for extra-pair copulations (Fraser & Stutchbury 2004; Norris & Stutchbury 2001).

The research to date clearly shows the importance of patch area in explaining richness, abundance and reproductive success for many species. Current research strongly supports the positive relationship between area and species richness. The relationship between abundance and area appears to be more complex.

Habitat patch shape has also been considered important for some birds since it relates more directly to the amount of interior habitat in the patch. In fact, for area sensitive birds, core area may be a stronger predictor than habitat patch area (Freemark et al. 1995). However, other studies have found that area variables are more important than variables describing the amount of habitat edge (what shape variables indirectly measure) for many native migrant bird species (Hawrot & Niemi 1996).

1.7 Birds, fragmentation and adjacent habitat

Researchers have not come to a consensus on the importance and relative influence of landscape-scale variables (such as the degree of fragmentation and the amount of habitat in the landscape) for birds. Furthermore, operationalization of landscape variables is convoluted and contentious. Programs such as FRAGSTATS (McGarigal & Marks 1995) can generate a multitude of variables to describe the surrounding landscape. I will concentrate on two commonly

researched quantifications of landscape variables: the amount of habitat in the landscape and fragmentation. Fragmentation is considered an operationalization of landscape configuration, which is a spatial effect, since it is considered separate from the concept and effect of habitat loss (see explanation in Fahrig 2003).

Many studies support the hypothesis that landscape-scale variables are important for understanding avian species distribution and diversity. Andrén's (1994) review of isolation factors suggested that isolation and island area are important factors for birds on oceanic islands. Mazerolle and Villard's (1999) more recent review of studies that investigated both patch and landscape variables for terrestrial habitat islands also concluded that landscape variables appear to be significant. Although not a meta-analysis, this review found that, of the twelve avian studies conducted in forest fragments embedded in agriculture, eight studies found that birds were sensitive to habitat configuration and six studies found that birds were sensitive to habitat cover in the landscape. They concluded that landscape-level variables appear to be important for some taxa such as birds. Villard et al.'s (1995) study of four migrant bird species in Ontario found that variables for landscape configuration (specifically, nearest-neighbour distance) were significant in logistic regression models of presence-absence data for three species. Robbins et al. (1989) found that the amount of forest within 2 km of the bird detection point was the second most important predictor of species abundance after forest area for neotropical migrants. However, four of these nineteen species with a significant relationship to forest cover in the landscape exhibited a negative relationship.

The above studies also highlight that for landscape variables the responses differ between species. Birds have been found to aggregate in their relationships with landscape variables such that species with the same migration strategy tend to have similar responses to landscape variables (Hinsley et al. 1995). For example, Flather and Sauer (1996) found that models of abundance for neotropical migrants included many landscape variables whereas short-distance migrants and resident species had significantly fewer landscape variables in their associated models. Other studies concur with the hypothesis that different guilds of birds respond differently to landscape variables and that neotropical migrants may be more sensitive than other species groups (Pino et al. 2000; Robbins et al. 1989). Birds categorized as interior species also have stronger relationships with landscape variables. Austen et al. (2001) found that interior species had significant, positive relationships with local forest cover (within 2 km), while interior-edge and edge species had nearly significant and negative relationships with local forest cover. Lee et al. (2002) hypothesized that differences in life history traits may be responsible for observed different responses to landscape variables.

Some studies compared the relative importance of landscape configuration and the amount of habitat in the landscape for birds. The hypothesis emerging is that the amount of habitat in the landscape appears to be more important for predicting species distribution and

diversity than the spatial organization of this habitat (Cushman & McGarigal 2004; Fahrig 2003). For example, Westphal et al.'s (2003) study in Australia found that individual bird species responded consistently and strongly to the amount of habitat in the landscape and responses to landscape configuration were inconsistent. A similar comparison has been found between landscape composition and fragmentation where the amount of habitat in the landscape has been found to be more important for more species than the degree of fragmentation (Trzcinski et al. 1999). However, other studies have shown contrary results; Villard et al. (1999) showed that landscape configuration and forest cover were equally significant predictors for avian logistic regression models.

Increasingly, more research supports the hypothesis that landscape scale variables, although important for birds, are less important than habitat patch variables (Cushman & McGarigal 2004). For example, in a survey of small woodlots in England, Bellamy et al. (1996) concluded that variables describing the habitat itself (vegetation variables as well as forest size) predicted woodland bird richness much better than landscape variables, although landscape variables were still considered important. This study included a number of landscape variables describing connectedness, isolation, and surrounding land-use.

The complex interrelationship between variables (e.g. correlation or interaction effects) at different spatial scales affecting avian distribution can confound conclusions. Lee et al. (2002) cautioned in their study of patch versus landscape variables that the strong correlation between patch size and the amount of forest in the landscape may have led to erroneous conclusions in previous studies about the relative importance of patch size. To clarify the relationship between different variables that may affect bird distribution, Riffell et al.'s (2003) study of birds in Great Lakes coastal wetlands removed the correlation between patch and landscape variables through regression techniques. They found that landscape variables significantly explained between 5-46% of the variation in individual abundance models. Although a broad range, this percentage seems consistent with the general conclusion that landscape variables, although more important for some species, may only be secondary factors in explaining species abundance and richness patterns (Westphal et al. 2003).

Several studies suggested that the relative importance of landscape variables may vary with the type of landscape. Andrén (1994) proposed that isolation of forests and forest areas were important variables when the amount of habitat in the landscape reaches a lower level of 10-30%. Similarly, some studies that have found no relationship between landscape variables and bird distribution suggested that their conclusions may be due to the abundance of habitat in the landscape or that the natural matrix has a different effect on bird species than human-dominated surrounding landscapes (Berry & Bock 1998; Crozier & Niemi 2003). Others counter that these hypotheses have not been empirically demonstrated (Fahrig 2003).

1.8 Birds and the matrix

The number of investigations including the matrix as an element of the landscape that influences species distribution has been slowly increasing. Metapopulation models often assume that the matrix is hostile non-habitat (Andrén 1994). For many species, the matrix is not absolutely hostile, depending on the matrix type (Desrochers & Hannon 1997 where some movement was recorded in matrix.). In most models of a complex landscape, movement through the matrix poses mortality risks for individuals (Fahrig 2001), but other species have been found to exploit resources in the matrix (Bayne & Hobson 1997). Different matrix types likely affect species in different ways (Bayne & Hobson 1997; Rodewald 2003; Rodewald & Yahner 2001).

Individuals may still be affected by the matrix even if they do not leave their habitat patch; a matrix can harbour elements that may affect species. For example, urban areas can increase domesticated predators and human activities in natural areas that lower avian species diversity (Bayne & Hobson 1997; Odell & Knight 2001). Our understanding of the effect of the matrix is complicated by the different types of land-use that may occur within it, as well as the species' vulnerability to this land-use.

1.8.1 Birds and an urban matrix

A review of the pertinent literature discovered that avian studies related to urbanization can be categorized as studies that investigated (1) birds using remnant habitat within or adjacent to an urbanized matrix (here it is treated as a landscape effect) or (2) birds using altered habitat within the urban matrix (such as plantings in parks or suburban areas). In the former group, the researchers used urban variables as another human disturbance in the landscape, such that they assumed that urbanization acts as a type of matrix effect. Although based in different perspectives, the conclusions of these two approaches complement each other. This study will focus on urbanization as a landscape effect.

Recent research revealed the complexity of urban systems and species' responses to it, but some general conclusions have emerged. Typically, comparisons between urbanized areas and habitat in non-urbanized areas find that there is a greater abundance of birds in urban areas, but there are fewer species (richness decreases)(Beissinger & Osborne 1982; Emlen 1974; Horn 1985). As Beissinger and Osborne (1982) explained, few bird species dominate urban habitats and they are typically non-natives that rapidly colonize and reproduce. Similar to other studies, they found a significant decline in species richness in urban areas, and they concluded that most of the missing species were associated with forests.

In urban areas, as in non-urban areas, birds respond to a complex combination of environmental factors (Germaine et al. 1998). Neotropical migrants have been found to be sensitive to urbanization (Friesen et al. 1995; Nilon et al. 1995). Odell and Knight (2001) found a similar trend, but they noted that they could not find any trends in species' life history

characteristics that would explain the adaptability of the non-native birds to urban development. They suggested that the “human-sensitive” species may be particularly sensitive to the fragmentation that occurs in urban areas and the consequent exposure to brood parasites (such as brown-headed cow birds, *Molothrus ater*). Other life history characteristics, such as ground nesting, may make birds susceptible to domesticated pets and other factors associated with urban development (Kluza et al. 2000; Maestas et al. 2003; Miller et al. 2003). Urban areas may also favour birds that exploit a certain food source such as seeds (Emlen 1974).

Many urbanization studies have been situated in the western United States, and their results may have limited applicability to eastern North America since the relationship between avian species and urban development may depend on the surrounding ecology (Clergeau et al. 2001). As well, as Cam et al. (2000) emphasized, the shape of the relationship between species richness and urbanization likely depends on the approach to quantify urbanization.

The effect of urbanization must also be untangled from other explanatory variables (Rodewald 2003). Many variables are likely confounded with urbanization. For example, local vegetation consistently appears as an important confounding variable. In Australia, Munyenyembe and others (1989) found that species richness was strongly correlated with the percent cover and foliage height of native vegetation. Other studies in urban areas supported this relationship (Clergeau et al. 1998; Melles et al. 2003; Mills et al. 1989). Some researchers claimed that their analysis shows a significant effect of urbanization above and beyond local vegetation variables (Bolger et al. 1997; Odell & Knight 2001), but the nature of the relationship between these variables should be unraveled in order to understand the true effect of urban development.

Regardless of the complexities of understanding urbanization, this variable has been found to be important for predicting bird species distribution and diversity. Bolger et al.’s (1997) study in coastal shrub found that the abundance of half of the 20 species significantly correlated with position to development, independent of local habitat variables. Haire et al. (2000) surveyed grassland birds around Bolder, Colorado and they found a general negative trend between individual species abundance and their urban index. Also, Miller et al.’s (2003) study of native birds in riparian areas found that settlement intensity best explained variations in habitat use, although local habitat variables were still important. Of the few landscape-scale urban studies in forests, Mörtberg (2001) found that the percent built area in the landscape was significant for coniferous forest birds in Sweden. However, the percent forest in the landscape was significant for all species.

These studies generally considered urbanization as one factor among other habitat patch and landscape variables potentially affecting bird species. Few studies have investigated the relative effect of urbanization compared to the other variables. Some studies tentatively suggested that urbanization may not be as important as local variables (Melles et al. 2003), or that the observed effect of urbanization may be due to other confounding factors such as vegetation (Miller et al.

2003). Furthermore, the conclusion that landscape variables are less important than habitat variables also applies to the effects of the urbanized matrix. However, as McGarigal and McComb (1995) suggested, different matrix types may affect this relative importance of landscape and patch variables. For example, a study in Ontario by Friesen et al. (1995) suggested that the magnitude of effect of urbanization may be comparable to the effect of habitat area. Friesen summarized his research of urbanization effects on neotropical migrants (1998) and he emphasized that “the impact of residential housing on these birds was only slightly less extreme than the removal of forests altogether.” It appears that more research is needed to determine the most important variables for birds in urban areas.

1.9 Summary of literature review

Theory and on-going research in landscape ecology suggests variables that may explain bird species abundance and richness when quantified for landscapes. Habitat area emerges as an important variable positively associated with measures of abundance and richness as well as breeding success. The amount of habitat in the landscape and fragmentation appear to be important for some species, although there is more variability in their significance for abundance and richness measures. Some research also suggests that these variables may be less important than habitat area. These tentative conclusions have largely been drawn from non-urban areas. Urbanization may have a profound effect on some bird species. As a matrix effect, it is significant for abundance and richness measures in many studies.

The above summary suggests the relative importance of variables found in the literature to explain avian diversity. These statements can be viewed as competing hypotheses describing the most important factors for avian richness and abundance:

- 1) The area of the habitat patch is the strongest predictor of avian diversity.
- 2) Variables describing the habitat patch itself are most important, including habitat area and vegetation descriptors.
- 3) The area of the habitat patch is important, but landscape variables should also be considered. In this, the amount of habitat in the landscape may be more important than fragmentation.
- 4) Urbanization is an important variable over and above the importance of the habitat area.

The next section will explore the translation of these hypotheses into mathematical statements with defined variables.

2.0 Methods: Temporal and geographic scope of study

This study is situated in the Greater Toronto Area (Figure 2.1), a major population centre in southern Ontario, located at 43.67°N 79.63°W at a height of 173m above sea level. The actual study area is the jurisdiction of the Toronto and Region Conservation Authority (TRCA), which encompasses the watersheds of the Greater Toronto Area. The average yearly temperature is 7.3°C with an average rainfall of 765.5mm per year (Buttle and Tuttle Ltd. 2004). The central business district of Toronto is located on the shores of Lake Ontario. The surrounding municipalities of the Regional Municipalities of Peel, York and Durham flank the City of Toronto to the west, north and east and these municipalities compose what is known as the Greater Toronto Area.

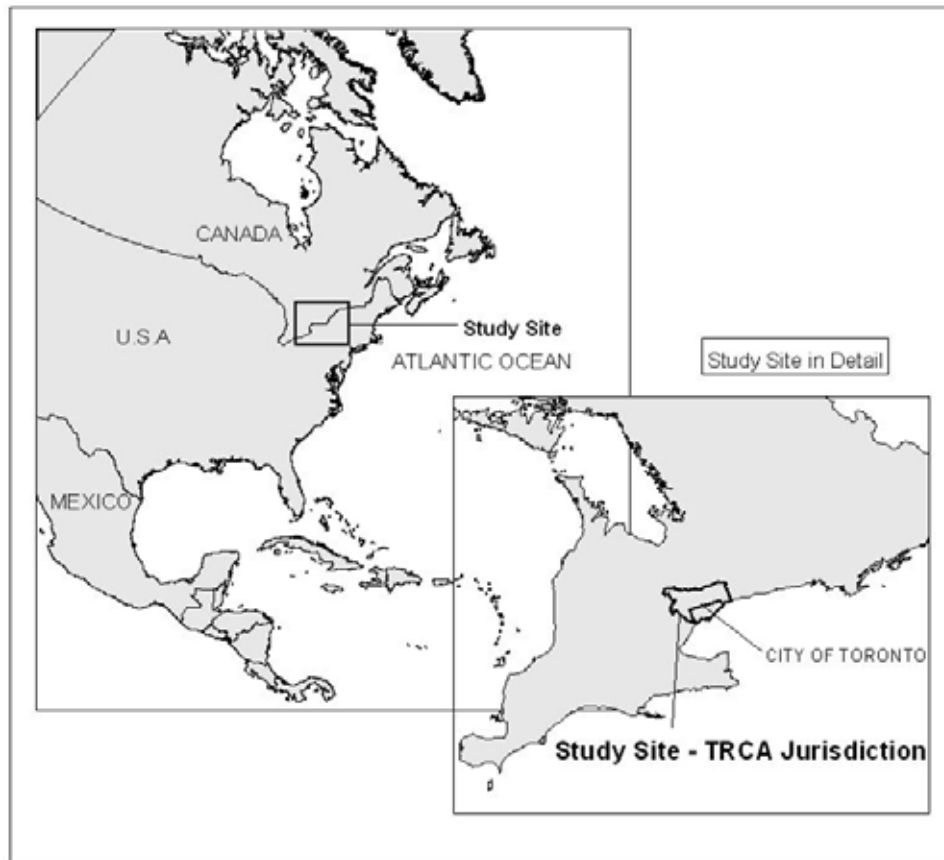


Figure 2-1: Location of study site within a North American context.

(Environmental Systems Research Institute Inc. 1992, 1993)

The Greater Toronto Area is located in the Great Lakes - St. Lawrence Deciduous Mixed Forest zone. Species such as sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and white ash (*Fraxinus americana*) often dominate the deciduous forests while conifers such as eastern white cedar (*Thuja occidentalis*), eastern hemlock (*Tsuga canadensis*) and white pine (*Pinus strobus*) are also common.

The geographic and species information used in my study was collected by staff at the TRCA, the body responsible for watershed planning in much of the Greater Toronto Area. The TRCA jurisdiction of 3,467 km² covers a large portion of the Greater Toronto Area, including nine major watersheds that have their headwaters in the Oak Ridges Moraine, located to the north of the City of Toronto (Figure 2.2). This jurisdiction creates the study boundary.

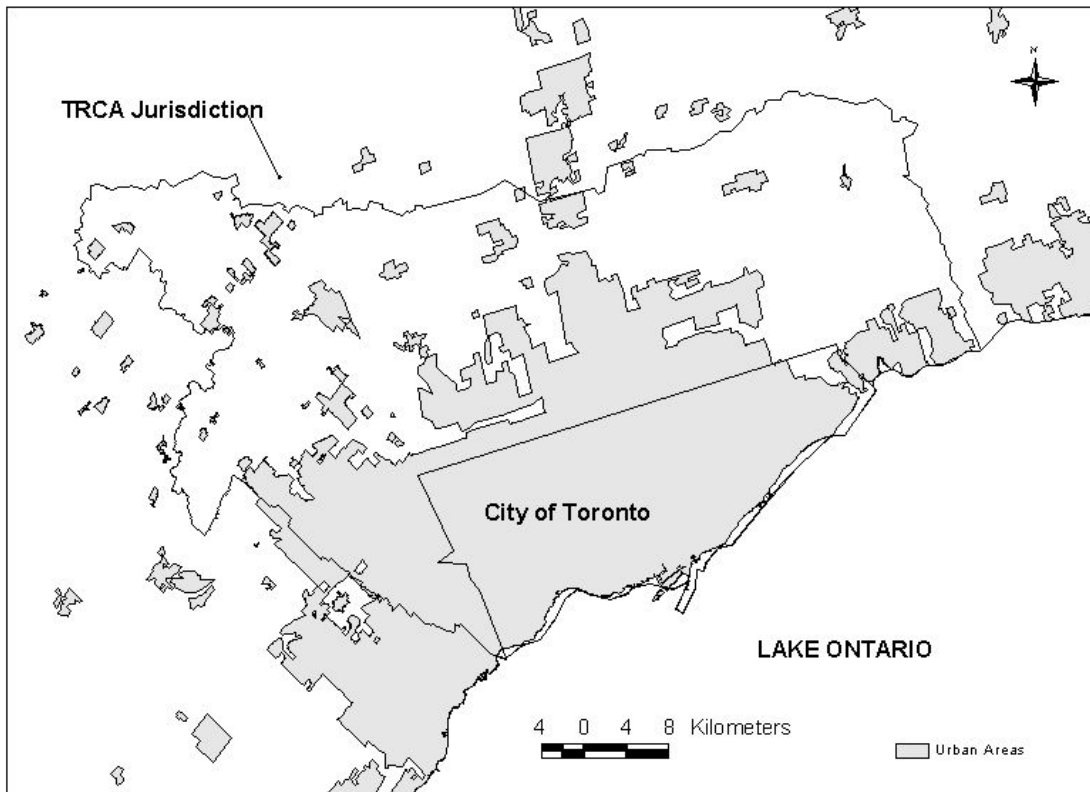


Figure 2-2: The study site boundary corresponding to the Toronto and Region Conservation Authority jurisdiction.

Since 1995 the TRCA has collected breeding bird data throughout their jurisdiction. Since 2000 this project has been increased so that approximately 4000-8000 ha of natural area is surveyed each year by trained biologists. To date, approximately 50% of the natural area within TRCA's jurisdiction (including public and private lands) has been subject to detailed surveys of both flora and fauna (Toronto and Region Conservation 2002). This data collection is a part of a large project at the conservation authority called the Terrestrial Natural Heritage Program (Toronto and Region Conservation 2004). It aims to assist in small scale decisions related to the municipal plan review process and to TRCA's conservation land planning (Toronto and Region Conservation 2002). The following sections detail the information in the database.

2.1 Geospatial Database

The data collected by TRCA staff is stored in a GIS-based database, and it is composed of detailed terrestrial information. Data is formatted in NAD27 (zone 17) as shapefiles in ArcView GIS 3.2 format. From this database, I have been given permission to use point information on breeding birds, detailed vegetation community information, and landscape-level information (obtained from aerial photograph interpretation). Species and vegetation community information is collected and added annually to this database with the ultimate goal of assessing the whole jurisdiction. Assessed areas do not generally have more than one season's data. The landscape level vegetation data is based on 1999 orthorectified digital air photos.

2.1.1 Breeding bird point data

Breeding bird data is collected annually by trained staff for the TRCA natural heritage database. The collection methods follow a general procedure specified by internal protocols (Iwanyki 2004). The specific procedures indicate the strength of the sampling method and dictate the information available in the database for analysis.

During the breeding season (approximately early June to mid-July), biologists survey a set number of areas that have been identified for that year as representative natural area in the jurisdiction. For each year, there is an attempt to select sites representing all parts of the jurisdiction. Biologists survey the sites at least twice during the breeding season with the first visit occurring during early June and the second visit occurring in late June or early July. Bird songs are most pronounced in Ontario from late May to mid-June and most species are attending young in or out of the nest by early-July (Cadman et al. 1987). Third visits, if possible, typically occur within the first half of July (Toronto and Region Conservation 2003:21). Surveys start before sunrise and continue until later morning (approximately 11am), although not in times of high wind or heavy precipitation (Toronto and Region Conservation 2003:24).

The procedure requires trained biologists to walk transects of the habitat patch in order to cover the whole area within hearing distance. The biologist determines the walking route through the area that will allow audio access to as large a proportion of the site as possible (Prior 2004). For some species, biologists use tape-playbacks of songs. On the second visit, biologists attempt to walk the same route but at a different time of the morning. This method is based on survey protocols for the Ontario Breeding Bird Atlas (Cadman et al. 1987).

The breeding bird surveys identify all singing males in the delineated sites, but only birds deemed sensitive by the agency are mapped at a specific location. This limits the number of species included in the database and, consequently, in my analysis. Included species are considered to be of "conservation concern". This categorization is based on a scoring system that gives each species a

numerical score based on their understood characteristics in each of the following categories: local occurrence, national or continental population trends, local population trend, habitat dependence, mobility restrictions, area sensitivity, and sensitivity to development (Toronto and Region Conservation 2003).

The biologists record breeding sightings as either possible, probable or confirmed, according to the terminology in the Ontario Breeding Bird Atlas (Cadman et al 1987). All sightings recorded as probable or confirmed are guaranteed to be entered into the database. Possible breeding records are assessed on their individual merit by fauna biologists at the TRCA. Possible breeding designation indicates that the species was observed in its breeding season in suitable nesting habitat or that a singing male was heard in suitable breeding habitat. As a result, the bird records represent, at least, territorial males in appropriate breeding habitat (Prior 2004). Therefore, the bird points in this database do not only represent breeding bird status in terms of breeding or reproductive success.

2.1.2 Vegetation community data

Coinciding with the collection of breeding bird information, staff at the TRCA collect vegetation community information and flora species data. Each year, the same sites identified for the collection of breeding bird data are surveyed for vegetation community information. Biologists with botanical expertise survey natural areas for this data. These surveys occur from May to October (Toronto and Region Conservation 2003:9-13).

Vegetation communities are identified using a modified procedure and classification based on the Ecological Land Classification (ELC) for southern Ontario (Lee et al. 1998). Biologists at TRCA are trained in the ELC procedure. ELC provides a coding system to classify all vegetation communities of southern Ontario based on the dominant vegetation in the canopy layer. The modified TRCA survey has also included additional codes for forests, treed swamps and plantations that described unique communities composed of non-native tree species (e.g. Manitoba Maple, *Acer negundo*).

My study focuses on treed habitats including forests, treed swamps and plantations. Table 2.1 outlines the codes for the different treed habitat types used in my investigation, as designated in the Ecological Land Classification for Ontario (Lee et al. 1998).

Table 2-1: Description of treed habitats considered in study (as described in the Ecological Land Classification (ELC) system for southern Ontario (Lee et al 1998) and as adopted by TRCA).

Habitat Type	Description	ELC code*
Deciduous forest	Canopy cover greater than 60%; greater than 75% cover of deciduous trees.	FOD
Coniferous forest	Canopy cover greater than 60%; conifer tree species greater than 75% of canopy cover	FOC
Mixed forest	Canopy cover greater than 60%; conifer species and deciduous species each greater than 25% of canopy cover	FOM
Deciduous Treed Swamp	Tree cover greater than 25% and deciduous species greater than 75% of canopy cover. Soils, hydrology and species indicate wetland conditions.	SWD
Coniferous Treed Swamp	Tree cover greater than 25% and coniferous species greater than 75% of canopy cover. Soils, hydrology and species indicate wetland conditions.	SWC
Mixed Treed Swamp	Tree cover greater than 25%; deciduous and coniferous species each greater than 25% of canopy cover. Soils, hydrology and species indicate wetland conditions.	SWM
Cultural Plantation	Tree cover greater than 60%; community resulting from or maintained by human disturbances.	CUP

* The ELC code is for the “community series” that are “units that are normally visible and consistently recognizable on air-photos” (Lee et al. 1998:18).

Species such as sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and white ash (*Fraxinus americana*) often dominate the deciduous forests while conifers such as eastern white cedar (*Thuja occidentalis*), eastern hemlock (*Tsuga canadensis*) and white pine (*Pinus strobus*) are common in coniferous forests. Treed swamps can be dominated by deciduous species such as red maple (*Acer rubrum*) or black ash (*Fraxinus nigra*) or coniferous species such as eastern white cedar (*Thuja occidentalis*). Cultural plantations are resulting from or maintained by human disturbance, and they can contain native or non-native species (Lee et al. 1998).

Biologists survey the sites for vegetation by systematically walking through the delineated area. Trained biologists describe and map the vegetation communities based on the dominant species in the canopy (Toronto and Region Conservation 2003:12). Communities are classified to a much finer scale than the community series designations presented in Table 2.1.

2.1.3 Remote-sensing data

The TRCA has also delineated vegetation types from digital air photo interpretation for the whole jurisdiction. All of the natural area within the jurisdiction has been separated into forest, wetland, native meadow and coastal areas (Toronto and Region Conservation 2004:8). The TRCA has compiled this information in order to calculate landscape-level measures such as forest patch

shape and natural cover (Toronto and Region Conservation 2003:2). I used this information to refine the urbanization variable (Section 2.2.6).

2.2 Variables

All of the variables used in building models to describe species richness and abundance were derived from the data layers in the TRCA database. Most of the variables were created through manipulations in ArcView 3.2 (Environmental Systems Research Institute Inc. 1999) using scripts programmed in Avenue, ArcView’s internal object-oriented language. The specific variables chosen for the modelling exercise were identified as important predictors of bird distribution (see Section 1). A visual depiction of the main variables is presented in Figure 2-3.

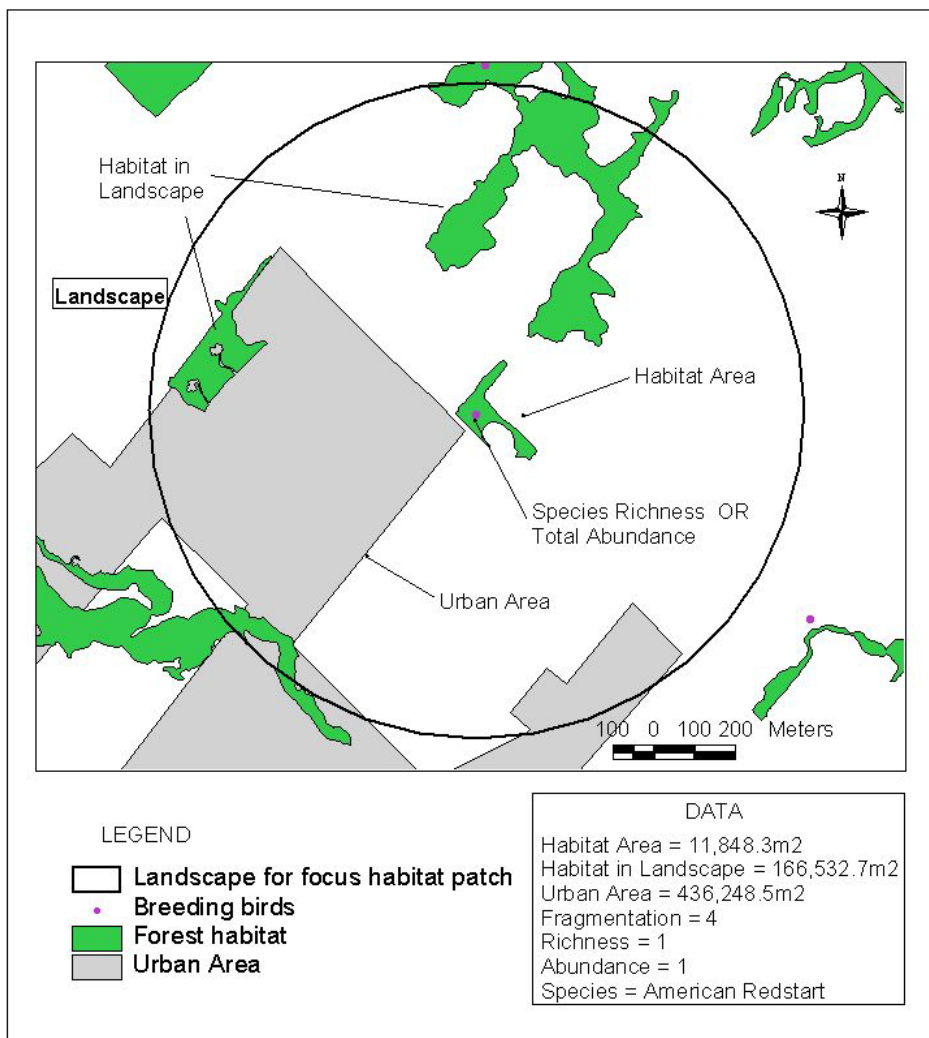


Figure 2-3: Demonstration of how variables are calculated in the GIS database.

2.2.1 Patch Area

TRCA's database separates all vegetated areas into vegetation community classifications. In order to make these areas relevant for the species of interest at the landscape scale, the connected vegetation communities were amalgamated into patches and distinguished from non-habitat (as suggested by Li & Wu 2004). This gives ecological relevance to the landscape indices generated from this vegetation cover data since the area of natural vegetation in the landscape is identified as habitat for the focal species. The two habitat designations were forests (See Table 2.1: FOD, FOC and FOM) and all treed habitats (See Table 2.1: FOD, FOC, FOM, SWC, SWD, SWM, CUP). The forest category was for birds that were specified to use only upland forested habitats and the treed habitat was for birds using all forest types. Using two habitat types should tailor the distinction between habitat and non-habitat for different bird species.

Habitat patches were modified to reflect current understandings of avian use of habitat. Following the procedure of Villard et al. (1995), areas connected by a corridor width of less than 30m were separated and the corridor eliminated from analysis. It is assumed that birds are unlikely to use these corridors for habitat, so the effective area of a patch should not include them. I also employed a minimum distance measure between patches. It is assumed that forest-specialist birds are unlikely to have territories encompassing gaps of greater than 30 m (Villard et al. 1995). I selected forest patches that were isolated from other patches by 30 m or more. Numerous landscape studies of birds have employed this site selection technique (e.g. Austen et al. 2001; Friesen et al. 1995). The remaining habitat patch was measured in square meters. All patches greater than 0.5 ha were included in the analysis since this is the minimum size identified in the ELC procedure (Toronto and Region Conservation 2003:9).

It is possible that this site selection method can potentially bias the sample so that these isolated forests are not representative of the larger sample of woodlots within the jurisdiction. To compensate for this potentially erroneous assumption, two groups of woodlots were investigated: those chosen with a minimum distance criterion of 30m and those chosen without a distance criterion.

Habitat shape or core area variables were considered but later abandoned since the range of habitat patch sizes was not sufficiently large to make core area a meaningful variable. Furthermore, it was assumed that habitat patch area would sufficiently capture the ecological relationship between patch geometry and bird diversity.

2.2.2 Landscape Area

Opinions differ as to what defines the scale for a landscape. In general terms, a landscape can be defined as a "land surface and its associated habitats at scales of hectares to many square kilometers" (Turner & Gardner 1991). Following the approach of many North American landscape studies, I have scaled the size of the landscape to the focal organisms. For birds, the landscape is

generally identified as an area larger than the species territory, but within the range of dispersal activities (Lee et al. 2002). Following the procedure of Lee et al. (2002) for a similar study in Ottawa, Ontario, landscapes of 800 m radius (201 ha) were chosen. This area was selected because the landscape area is likely to encompass the focal species' territory and mark-recapture evidence from Ontario shows that most North American species rarely moved beyond 200 m from their mark site even after several breeding seasons (Villard 1991 Ph.D. thesis, as quoted in Lee et al. 2002). Other studies have used similar landscape areas, ranging from 1-2 km in radius (Austen et al. 2001; Berry & Bock 1998).

2.2.3 Amount of Habitat in the Landscape

The amount of habitat in the landscape has been clearly identified as an important variable for predicting avian distribution (Cushman & McGarigal 2002). This variable is simply represented by the amount of identified habitat (including the patch area) present within the landscape boundary (in square meters). To be as accurate as possible in identifying habitat for the focus species, the field-surveyed vegetation community shapefile based on ELC was used to quantify this variable (see Section 2.1.2). The coverage of this shapefile was examined to ensure that all areas within each landscape had been surveyed in the field. In the treed analysis, the remote sensed forest information was used to supplement areas in which there was no ELC vegetation community identification. This was not completed for the forest habitat analysis because it would largely overestimate this variable.

2.2.4 Proximity Measure

Many landscape configuration measures exist to operationalize proximity of adjacent habitat to the focal habitat patch. Bender et al.'s (2003) review of proximity measures recommended area-based measures as robust measures for simulated and real landscapes. In this procedure, the variable is measured as the area of habitat within a specific buffer distance. Bender et al. (2003) emphasized the importance of choosing buffer distances that are appropriate for the dispersal capability of the study organisms. In my study, the landscape size of 800 m was maintained for this measure. Therefore, the habitat in the landscape variable also represents a proximity measure.

2.2.5 Fragmentation Measure

As defined earlier, fragmentation is considered to be the breaking apart of habitat. There are many ways in which fragmentation can be operationalized including quantifications of the amount of edge area (see examples in Cushman & McGarigal 2004). In my study, fragmentation was quantified as the number of patches in the landscape. In a recent review of the fragmentation variable, Fahrig (2003) summarized various operationalizations. Average patch size was the most prevalent measure. I have already used this variable as the measure of habitat area. Fahrig also emphasized the interrelation between fragmentation measures. To limit the number of variables and the overlap between variables, I have represented fragmentation in as few measures as possible. Therefore, the number of patches in the landscape was chosen as one variable to operationalize

fragmentation; it is likely strongly related to and representational of other measures of fragmentation.

2.2.6 Urbanization measure

Urbanization has been operationalized differently by researchers, with variations in scale and description. The TRCA database contains data on urban areas. This is a crude measure of urbanization that identifies those areas designated as zoned for urban use by the respective municipality (Iwanyki 2004). For my study, the urban layer was used to quantify the amount of urban area (in square meters) in the landscape surrounding each habitat patch. This layer was further modified using the aerial photograph identified vegetation data (Section 2.1.3). These known vegetated areas were subtracted from the urban boundary layer. The remaining area was assumed to be composed of various types of urban development (e.g. roads, residential development and industrial development). The degree of urban development in this zone likely varies throughout the jurisdiction with some areas likely overestimating the actual amount of urbanization on the ground. This is one of the constraints of this rough urbanization measure.

2.2.7 Floristic measure

Miller et al. (2003) found from their investigation of the effects of urbanization and vegetation variables on bird distribution that urbanization had an indirect effect on birds through changes in vegetation. A higher percentage of exotic vegetation is typically found in urban and suburban forests (Moffatt et al. 2004), and vegetation in urban areas has been found to be different from non-urban areas (Beissinger & Osborne 1982). In order to represent this change in vegetation and its possible effect on the response variable, a floristic value was generated for each focal patch. The variable describes the percent of exotic vegetation in the patch based on the area of the vegetation communities dominated by exotic canopy species that compose the focal patch. This variable does not describe the presence of exotic vegetation in other layers (such as the ground flora) since the ELC coding of vegetation communities is solely based on canopy species (Lee et al. 1998). The purpose of this measure is to account for an aspect of the vegetation characteristics of patches that has been noted as an alternative explanation for the observed effect of urbanization on birds.

In one study comparing the relative importance of patch level vegetation variables on avian species, the vegetation cover variable (e.g. percent of ground cover) was found to explain slightly more variance than the floristics variable. However, both variables explained considerably more variance than the vegetation structure variable (Cushman & McGarigal 2004). In this study, the vegetation composition variable was used instead of a vegetation cover variable, such as canopy closure, because it was felt that the database does not provide detailed enough information about the percent cover to distinguish between patches.

2.3 Site Selection

The TRCA database contains a large number of sites that could be used in my analysis. Their original choice of survey sites appears to be clustered, with complete surveys of all natural areas within the cluster; selection was based on priority areas as well as conscious representation (e.g. based on watersheds) throughout the jurisdiction. I conducted further site selection on this list of surveyed areas. Firstly, as noted in Section 2.2.1, areas of forest or treed area (depending on the analysis) were amalgamated into habitat patches that could be distinguished from adjacent areas of non-habitat. Figure 2-4 illustrates this exercise in the GIS interface. The first box shows the original evaluated vegetation communities. These represent forested areas that have different ELC codes as distinguished by differences in canopy composition. The merging of forested vegetation communities for this example patch would create the polygon in the second box. This is a simple amalgamation of the original vegetation communities. This new patch is considered a forested area.

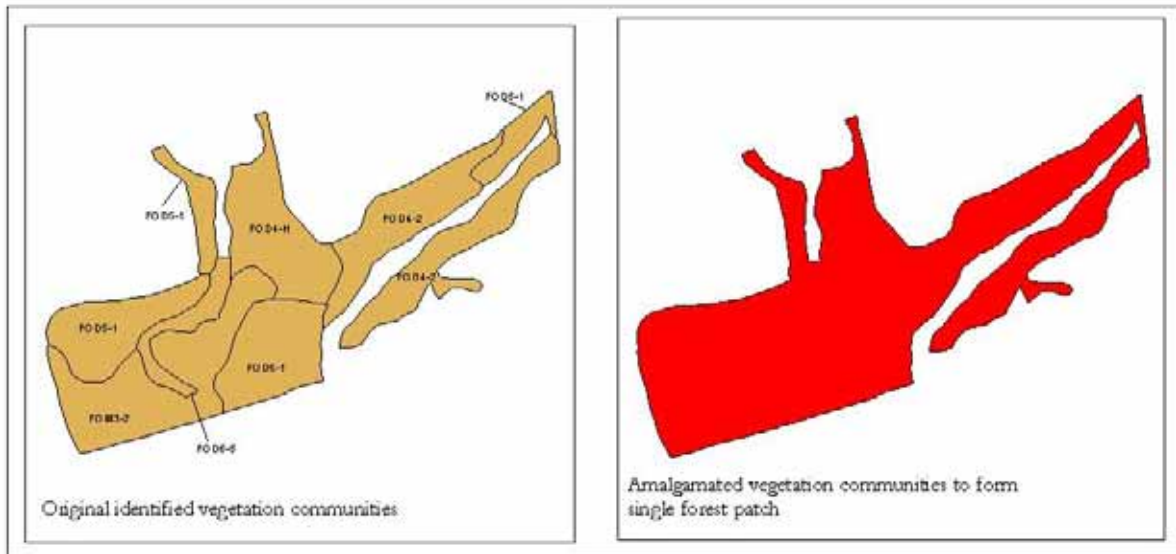


Figure 2-4: Illustration of habitat patch created through amalgamation of vegetation communities.

I also selected sites based on a distance criterion as described in Section 2.2.1. This created the final list of habitat patches available for modelling and analysis. All variables were calculated for these amalgamated patches.

2.4 Statistical Tests

The objective of this study is to determine which landscape elements are most important for describing avian species richness and abundance. A model building and comparison technique based on information theoretic was chosen to explore this research question. This approach is appropriate

because it allows for the investigation of complex ecological phenomena and the comparison of competing hypotheses to explain the relationships between avian diversity and landscape elements. The alternative step-wise consideration of numerous potential explanatory variables was deemed inappropriate and highly arbitrary (Burnham & Anderson 1998:17).

2.4.1 Background to the information theoretic approach

The information theoretic technique, often termed model selection or competition, is used to select among biologically relevant models to explain observed data. It has been heralded as a new paradigm for modelling species distribution. This “bottom-up” approach of model selection requires the researcher to develop ecologically relevant models for the study site and organism while remaining grounded in theory. This will create more robust models of greater utility (Rushton et al. 2004).

Model selection is based on Kullback-Leibler information. Outlined only briefly here, Kullback-Leibler information gives the discrepancy (“statistical distance”) between two models (Burnham & Anderson 1998). It is the logical basis for model selection as defined by Hirotugu Akaike (Akaike 1973 as cited in Burnham & Anderson 1998), and Akaike’s information criterion (AIC) used to select between competing models is based on this information between models. Akaike’s break-through was the discovery of how to minimize the expected estimated Kullback-Leibler information for a model selection process (Burnham & Anderson 1998).

The model selection approach has been recommended for field ecology studies as an alternative to traditional null hypothesis testing. It is increasingly used in biological research (Boyce 2002). Traditional null hypothesis and significance testing have been criticized on a variety of fronts. Anderson et al. (2000) stated that null hypotheses often represent biologically implausible statements and, therefore, are generally uninformative. Their search through the wildlife biology literature demonstrated that significance testing and quotes of P-values have been misused and abused. Anderson and Burnham (2002), vocal proponents in the wildlife biology literature for the model selection approach, emphasized the importance of null hypothesis testing in carefully controlled experiments that have randomized response and predictor variables. However, in observational studies that populate ecological research, model selection approaches are more appropriate (Anderson et al. 2000).

The model competition approach also attempts to create parsimonious models. Many studies that model species distribution favour a large suite of variables. This may be an attempt to account for all the possible contributing variables. Unfortunately, in modelling, the number of candidate models increases with the number of predictors available and the ‘best’ model identified may depend critically on the route taken to find it (Rushton et al. 2004). The large number of variables in one context may cause “overfitting” of the model so that it performs well in the specific context in which it was developed, but it is not robust when used elsewhere (Rushton et al. 2004).

2.4.2 The Models: Building and comparison

The Akaike's information criterion (AIC) was used to compare competing models. This calculation related to Kullback-Leibler information is based in the maximized log-likelihood function (Anderson et al. 2000). The model where AIC is minimized is selected as the best for the empirical data at hand (Anderson et al. 2000). AIC's strength lies in its attempt to evaluate parsimony; models are penalized for the number of parameters.

The calculation for AIC is,

$$\text{AIC} = -2\ln(l(\Phi \mid \text{data})) + 2K,$$

where $\ln(l(\Phi \mid \text{data}))$ is the value of the maximized log-likelihood over the unknown parameter (Φ), given the data and the model, and K is the number of model parameters (Westphal et al. 2003). Evidence for the alternative models can best be assessed by rescaling AIC values such that the model with the minimum AIC has a value of zero; this is done by finding Δ_i , the difference between the AIC of the focal model and the minimum AIC (Anderson et al, 2000). Further analysis can normalize the values of the likelihood of fit of the models. This Akaike weight can be interpreted as the approximate probability that the specific model is the best of those considered (Anderson et al. 2000).

It is important to note that model competition is not a test in any sense; there is no notion of significance. Rather, there is the concept of the best inference given the data and the set of selected models (Anderson et al 2000). One of its strength lies in the use of the AIC measure which is robust, unbiased and rooted in the theory surrounding Kullback-Leibler information (Burnham & Anderson 1998).

2.5 Competing hypotheses

The model competition method described above requires the *a priori* demarcation of competing hypotheses. For this study, the hypotheses have been generated from the theory and literature describing the relative importance of landscape and patch variables for predicting avian species distribution, as described in Section 1 (e.g. Cushman & McGarigal 2004). Table 2.2 describes the competing hypotheses and relates each model hypothesis to the statement hypothesis found in Section 1.

Table 2-2: Models representative of competing hypotheses. A general model structure is provided to represent the variable relationship entered into the statistical software. Response is the measure of richness or abundance in the patch, Habitat Area is the patch area in square meters, Floristics is the floristic variables, Urban Area is the amount of urbanization in the landscape, Fragmentation is the fragmentation variable quantified as the number of patches within the landscape.

Hypothesis	Model Structure
1. The area of the habitat patch is the strongest predictor.	Response ~ Habitat Area
2. Only variables describing the habitat patch itself are most important	Response ~ Habitat Area + Floristics
3. The area of the habitat patch is important, but landscape variables are also important.	Response ~ Habitat Area + Habitat in Landscape Response ~ Habitat Area + Urban Area
4. In the third hypothesis, the amount of habitat in the landscape may be more important than fragmentation.	Response ~ Habitat Area + Habitat in Landscape + Fragmentation
5. Urbanization is an important variable, above the importance of habitat area.	Response ~ Urban Area Response ~ Urban Area + Habitat in Landscape + Fragmentation

2.5.1 Complex relationships between variables

In ecology, variables can have complex relationships to each other such as collinearity and interaction that can affect analysis and interpretation of statistical tests (Philippi 1993). In this variable selection, I attempted to choose a smaller number of variables in order to avoid problems of correlation that have plagued the landscape ecology literature (Fahrig 2003). Authors have particularly noted that the amount of habitat in the landscape and fragmentation have been two variables that tend to be strongly correlated (Trzcinski et al. 1999). To avoid this possible relationship, the overlap between these two variable was removed through linear regression (one method cited in Fahrig 2003). Following the procedure of Villard et al. (1999), residuals of the linear regression were then used to represent the variance of the fragmentation variable not explained by the habitat in the landscape variable.

Interaction effects were also assumed to be common due to the complex relationships between the chosen variables. Two interactions were considered through logical consideration: the interaction between habitat in the landscape and urbanization and the interaction between habitat area and habitat in the landscape. Rodewald (2003) cautioned that urbanization likely had an effect on the amount of habitat in the landscape since urban development is often associated with habitat loss. Habitat area and amount of habitat in the landscape are likely to be linked in the landscape since their magnitude may be affected by the same processes of habitat loss (Fahrig 2003).

2.6 Overview of tests, variables and models

For this study, two types of vegetation groupings were analyzed. Firstly, all forest areas were combined so that the habitat considered consisted of deciduous, coniferous and mixed upland forest (see Table 2.1). A second run of the model competition considered a broader definition of forest that included plantations and treed wetlands. Within each habitat analysis, sites were selected through two methods: with and without a selection distance criterion. Table 2.3 summarizes the model competition exercises.

Table 2-3: Overview of the model competition exercises.

Vegetation Selected	Site Selection Criteria	Response Variable	Independent Variables Considered
Upland Forests (FOD, FOM, FOC)	30 m minimum distance between sites	Species Richness	<ul style="list-style-type: none"> • Habitat in landscape • Area of habitat patch • Area of urbanization in landscape • Fragmentation (number of patches in landscape) • Vegetation (percent exotic vegetation communities)
		Total Species Abundance	
	No selection criterion	Species Richness	
		Total Species Abundance	
All treed areas including treed wetlands and plantations (FOD, FOM, FOC, SWD, SWC, SWM, CUP)	30 m minimum distance between sites	Species Richness	<ul style="list-style-type: none"> • Habitat in landscape • Area of habitat patch • Area of urbanization in landscape • Fragmentation (number of patches in landscape) • Vegetation (percent exotic vegetation communities)
		Total Species Abundance	
	No selection criterion	Species Richness	
		Total Species Abundance	

2.7 Assumptions

My study makes a number of important assumptions that will be explicitly addressed here. These assumptions generally fall into the category of sampling methodology and statistical models.

Since these data were collected by another agency, the specific procedure of data collection could not be controlled or carefully tracked. This study must assume that sampling effort was equal for each hectare of natural area surveyed. Sampling effort bias can affect the number of detected

species. If larger patches are sampled with less effort than smaller patches, then the effect of area may go undetected. Since qualified staff collected the data, it is appropriate to assume that there is some awareness of sampling effort bias. Furthermore, the TRCA sampling protocol makes staff aware of appropriate sampling techniques (Toronto and Region Conservation 2003).

Study sites within the TRCA jurisdiction are generally surveyed for a single year and comparisons between sites will compare areas surveyed for different years. Comparing this data assumes that there is no difference between years in the bird populations. Similar to the year effect, this study assumes that the different observers do not sample the sites differently; it is assumed that areas surveyed by different people can be compared. These two variables were coded for the data and tested using analysis of variance tests. Similarly, I assumed that for the majority of the study sites, the variables extracted from the database accurately represented the circumstances on the ground at the time of the bird surveys.

This study has focused on some very specific variables. In the model competition method, there is an emphasis on using carefully chosen and appropriate measures in order to avoid flooding models with variables. With this selection of a small number of variables, it is assumed that important variables were not neglected. It is also assumed that regional, larger-scale variables such as climate are consistent between study sites.

It is assumed that the chosen variables and landscape size are appropriate for the chosen species. The variables appear to be well supported in the literature for forest birds. The landscape size was chosen carefully to be within the range of those used by previous authors in the literature for landscape ecology studies of native North American birds.

Finally, it is important to note the specific focus of this study in order to outline its jurisdiction. For example, this study focuses on a small subset of all the birds found in the Greater Toronto Area. This suite of species has been limited by those species that were surveyed by the TRCA and species using treed areas. This means that conclusions are only specific to this group of species. Extrapolated conclusions to other bird species or taxonomic groups must be made with caution. Furthermore, it is important to note that this is not a study based on species reproductive success. The use of singing male data is assumed to be a good preliminary understanding of the effect of landscape and patch scale variables on birds using fewer resources than a labour-intensive breeding study. Furthermore, this efficient study method has allowed for a large database.

There are a number of assumptions present within the statistical approach. The statistical models assume that the study sites are independent. This was tested through plotting semivariograms of model residual values. Isotropy and stationarity of the data are assumed.

3.0 Results: Model type and model selection assessment

A model structure had to first be assigned to the data. Poisson models were used based on the following criteria: 1) the response variables (abundance and richness) are count data lacking a normal distribution and 2) the independent variables show an approximate Poisson distribution with a distinct right skew. Furthermore, Poisson distributions can still be used if count data does not exactly follow a Poisson distribution (Jager & Looman 1995). The models were built with the relevant variables in “R” statistical software (R Development Team, 2004). Null deviance, residual deviance and parameter estimates were generated for each fit of the specific Poisson model to the data.

The models generated for the competing hypotheses were typically overdispersed so a modified AIC, called QAIC, was used (Burnham and Anderson, 1998:53). This modification of the AIC based on quasi-likelihood simply requires the inclusion of the dispersion parameter in the AIC formula. The dispersion parameter was included as an additional parameter when finding K. The calculation of the Akaike weights follows the same procedure as found in Anderson et al. (2002).

3.1 Bird species present in analyses

The TRCA database only identified species considered of conservation concern. This limited the list of birds within the richness and abundance analysis. The birds included in the analyses were also limited by the type of habitat used for each analysis. To accurately portray individual bird use of habitat in the landscape, the vegetation types included in each analysis should be considered habitat for each bird species. Species with habitat requirements that were inappropriate for the focus habitat type were excluded from analysis. For example, if a species was included in the forest analysis that used agricultural fields to supplement its habitat then the amount of habitat in the landscape variable would underestimate the species’ use of the surrounding landscape. Table 3.1 describes the species included in each analysis and their general habitat requirements. At this landscape scale, microhabitat requirements were ignored.

Table 3-1: Description of the bird species included in the analyses. Habitat requirements are briefly outlined (all information found in “The Birds of North America” edited by A. Poole and F. Gill and supplemented by information in Cadman et al. 1987; see full citations in Table 4-1).

Common Name	Species	Habitat	Category*	Included in forest habitat analysis	Included in treed habitat analysis
American redstart	<i>Setophaga ruticilla</i>	Mature deciduous forest, but also mixed forests, successional woodlands.	NTM, AS	X	X
American woodcock	<i>Scolopax minor</i>	Nests in a variety of forests with openings.	SDM		X
Cooper’s hawk	<i>Accipiter cooperii</i>	In deciduous, mixed and evergreen forests	R	X	
black-and-white warbler	<i>Mniotilta varia</i>	Woodlands, second growth forests and mature forests.	NTM, AS	X	X
black-throated blue warbler	<i>Dendroica caerulescens</i>	In hardwood and mixed forests.	NTM, AS	X	X
black-throated green warbler	<i>Dendroica virens</i>	Coniferous forest, mixed forests and occasionally deciduous forests	NTM, AS	X	X
brown creeper	<i>Certhia americana</i>	Found in a variety of forests and treed wetlands.	R	X	X
golden-crowned kinglet	<i>Regulus satrapa</i>	Breeds in a variety of woodlands as well as plantations and swamps.	R		X
hermit thrush	<i>Catharus guttatus</i>	Uses a broad spectrum of forest habitat, both wet and dry habitats.	SDM		X
northern waterthrush	<i>Seiurus noveboracensis</i>	Breeds in wooded swamps, thickets and mixed and deciduous woods.	NTM, AS		X
ovenbird	<i>Seiurus aurocapillus</i>	In deciduous and mixed forests, but also can be in coniferous forests.	NTM, AS	X	X
pileated woodpecker	<i>Dryocopus pileatus</i>	Deciduous and coniferous forests	R, AS	X	X
pine warbler	<i>Dendroica pinus</i>	Breeds in upland pine forests and mixed forests. Will breed in deciduous forests if pine is present.	SDM, AS	X	X
ruffed grouse	<i>Bonasa umbellus</i>	Most abundant in early successional forests.	R	X	X

scarlet tanager	<i>Piranga olivacea</i>	Prefers mature deciduous woods, but also in mixed forests, successional woodlands and plantations.	NTM, AS	X	X
sharp-shinned hawk	<i>Accipiter striatus</i>	Breeds in stands of deciduous, mixed and coniferous forests	R		X
veery	<i>Catharus fuscescens</i>	Strong preference for riparian areas, but also deciduous forests, and mixed forests	NTM, AS	X	X
winter wren	<i>Troglodytes troglodytes</i>	Associated with moist forests, mostly coniferous.	SDM		X
wood thrush	<i>Hylocichla mustelina</i>	Uses a wide variety of deciduous and mixed forests.	NTM, AS	X	X
yellow-rumped warbler	<i>Dendroica coronata</i>	Breeds in coniferous forests, mixed forests and less common in early successional forests and deciduous forests.	NTM		X

* Migratory Strategy: NTM = neotropical migrant; R = resident; SDM = short-distance migrant; Conservation terms: AS = area-sensitive; as categorized by Freemark et al. 1995 for northeastern North America.

Species considered too infrequent in the analysis were also removed since their use of the area may be solely due to chance. Species appearing less than one percent of the time in the total species database for each analysis were removed.

3.1 Testing the forest habitat

This first analysis focuses on forested areas with richness and total abundance as the response variables. The vegetation communities included in this analysis were deciduous, coniferous and mixed forests. Each analysis type for the forest habitat is shown below.

3.1.1 Forests with no selection criterion

For this analysis, no selection criterion was applied to the study sites. Models were constructed and the independence assumption was tested with semivariograms (R Development Core Team 2004), at a distance of 5000 m, on the residuals of the quasipoisson models. Models were found to lack independence. Therefore, this analysis was abandoned.

3.1.2 Modelling species richness in forests with a selection criterion

This analysis differs from the above in that a selection criterion was applied to the original database (see Section 2.2.1). Semivariograms were used to test the spatial dependence of the residuals of the models (Appendix II). The data was considered to meet the independence assumption, so Poisson models were deemed appropriate. The distribution of study sites is shown in Figure 3-1.

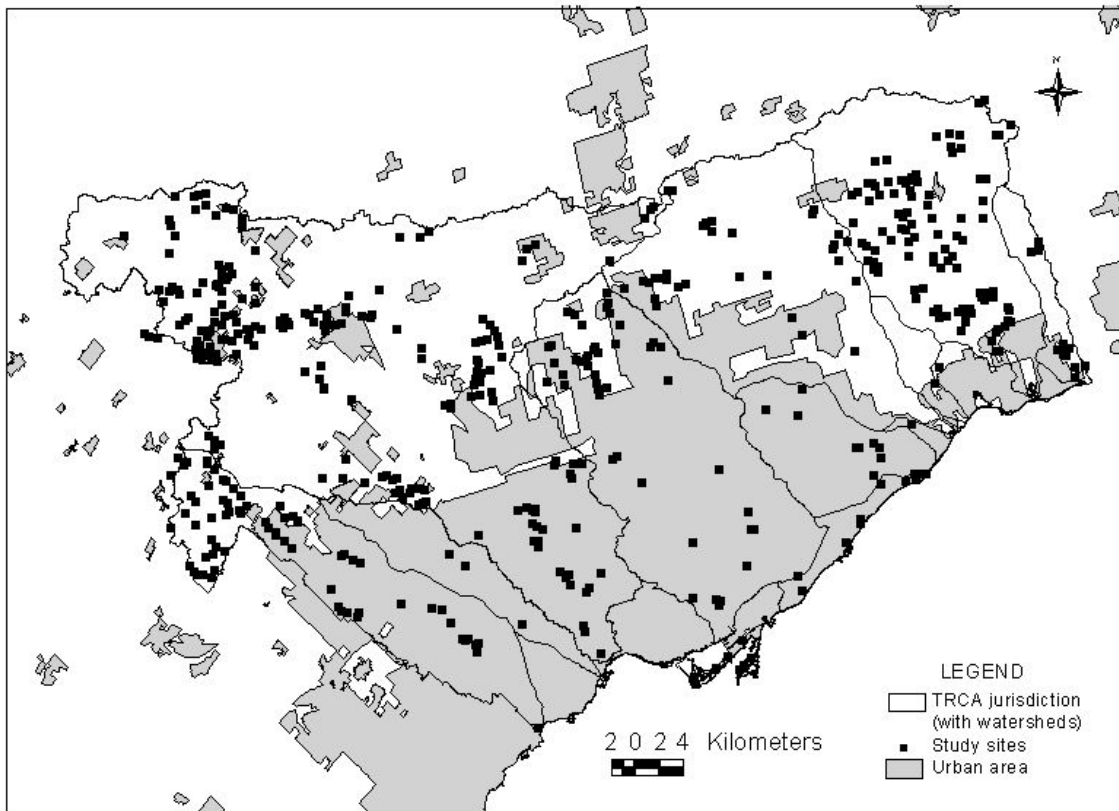


Figure 3-1: Location of forest habitat study sites.

The variables included in the analysis are described in Table 3.2. The majority of the explanatory variables are continuous with exceptions being the fragmentation variable and the two response variables: richness and total abundance.

Table 3-2: Description of variables included in the forest habitat analysis with a selection criterion.

Variable name	Symbol	Mean	Spread (Interquartile range)
Habitat Area	Ar	39,963 m ²	35,072.9 m ²
Richness	R	0.326	0*
Total Abundance	Ab	0.5443	0*
Floristics	Fl	0.098	0 [†]
Habitat in Landscape	La	190,310 m ²	167,936.7 m ²
Urban Area	Ur	437,697 m ²	879,517.6 m ²
Fragmentation	F	2.99	2

*See explanation below. [†] The zero spread for the floristics variable shows that most of the habitat patches are dominated by native habitat types.

Histograms of the variables are found in Appendix I. The zero spread for the response variables, richness and total abundance, results from the large number of habitat patches empty of any of the focal birds. A total of 171 patches out of the 485 have birds present. This proportion was still deemed sufficient to create the models, and the models did not show instability.

Three records were identified as outliers through visual scatter plots investigation of the relationships between the independent and dependent variables. These records were removed before subsequent analysis. The model competition with richness as the response variable is shown in Table 3.3. The models are ranked in ascending order based on QAIC values. QAIC, model differences and Akaike weights were calculated in MathCad (Mathsoft Engineering and Education Inc. 2002) and are detailed in Appendix III.

The model descriptions show the coefficients with significance levels for the parameters. The coefficients of the independent variable are interpreted in a similar fashion to regression coefficients in multiple linear regressions. They show the amount by which the dependent variable will increase if the independent variable changes by one unit (on a log scale according to Poisson model structure). A significant value for the parameter estimate indicates that it differs significantly from zero (Gotelli and Ellison 2004:250). Significance codes are shown at the bottom of the table.

Table 3-3: Results of the model competition using species richness for the forest habitat study sites with a selection criterion. The null deviance for the models is 601.27 with 485 records. The dispersion parameter for the full model is approximately 0.98. The letter “I” represents the intercept for the model. All other variable codes are described in Table 3.2.

Analysis Description	Models	Residual Deviance	K	QAIC	QAIC _i – minimum QAIC	Akaike weights
Richness ~ Urban Area + Habitat Area R ~ Ar + Ur	I = -1.44*** Ar = 1.235 x 10 ⁻⁵ *** Ur = -1.897 x 10 ⁻⁶ ***	369.81	4	385.2	0	0.99
Richness ~ Habitat Area + Habitat in Landscape + Fragmentation + Interaction between Habitat Area and Habitat in Landscape R ~ Ar + La + F + Ar*La	I = -3.24*** Ar = 3.00 x 10 ⁻⁵ *** La = 4.85 x 10 ⁻⁶ *** F = 0.22*** Ar*La = -5.21 x 10 ⁻¹¹ ***	376.21	6	395.7	10.5	5.2 x 10 ⁻³
Richness ~ Habitat Area + Habitat in Landscape + Interaction between Habitat Area and Habitat in Landscape R ~ Ar + La + Ar*La	I = -3.02*** Ar = 2.71 x 10 ⁻⁵ *** La = 4.46 x 10 ⁻⁶ *** Ar*La = -4.61 x 10 ⁻¹¹ ***	394.36	5	412.2	27.0	1.3 x 10 ⁻⁶
Richness ~ Habitat Area + Floristics R ~ Ar + Fl	I = -1.77*** Ar = 1.35 x 10 ⁻⁵ *** Fl = -2.10*	418.71	4	435.1	49.9	1.5 x 10 ⁻¹¹
Richness ~ Habitat Area R ~ Ar	I = -1.90*** Ar = 1.41 x 10 ⁻⁵ ***	431.44	3	446.0	60.9	6.1 x 10 ⁻¹⁴
Richness ~ Urban Area + Habitat in Landscape + Interaction between Urban Area and Habitat in Landscape R ~ Ur + La + F + Ur*La	I = -1.13*** Ur = -1.91 x 10 ⁻⁶ * La = 2.12 x 10 ⁻⁶ ** F = 5.49 x 10 ⁻² (NS) Ur:*La = -1.15 x 10 ⁻¹² (NS)	488.52	6	510.3	125.1	6.9 x 10 ⁻²⁸
Richness ~ Urban Area R ~ Ur	I = -6.194 x 10 ⁻¹ *** Ur = -2.251 x 10 ⁻⁶ ***	506.44	3	522.5	137.4	1.5 x 10 ⁻³⁰

Significance codes: *** P<0.001; ** P<0.01; * P<0.05; • P<0.1 ^{NS} P>0.1

The best model in this model competition to describe species richness includes the variables for habitat area and the amount of urbanization in the landscape with a QAIC of 385.2. The Akaike weight for this model is 0.99, clearly showing that $R \sim Ar + Ur$ is the best Kullback-Leibler information model for this set. This model accounts for approximately 39% of the null deviance. The second best model includes the habitat area variable and the other landscape variables: the amount of habitat in the landscape and fragmentation. The difference between the QAIC of this model and the QAIC of the best model is 10.5. This value is only slightly greater than the rule-of-thumb cut-off value of 10 that gives strong evidence that the second model is not competitive with the best model (Burnham & Anderson 1998).

The sign (positive or negative) of the coefficient shows the type of relationship between species richness and the other variables. Habitat area, amount of habitat in the landscape and fragmentation are positively related to species richness. The amount of urbanization in the landscape and the amount of exotic vegetation communities in the habitat patch (floristics variable) have a negative relationship with species richness.

Two interactions were considered in the model competition. The interaction between habitat area and the amount of habitat in the landscape is significant and negatively related to species richness. The interaction between the amount of urbanization in the landscape and the habitat in the landscape is not significant.

3.1.3 Modelling total abundance in forests with a selection criterion

The second analysis involving total abundance as the response variable is shown in Table 3.4. This analysis used the same dataset as the previous analysis so the variable distributions (Table 3.2) and outliers removed were the same. As well, coefficients and model selection analysis tools are similarly defined.

The total abundance analysis shows a different model as the best model in the comparison set. The model including the habitat area and the other landscape variables (amount of habitat in the landscape and fragmentation) plus an interaction term between habitat area and the amount of habitat in the landscape is the best model with a QAIC of 421.4. The next model in the ranking is the best model in the previous analysis ($R \sim A_r + U_r$). It has a QAIC value of 425.2. The second best model differs by 3.7 units from the best model, and this is barely within the rule-of-thumb range for weak evidence that this model is not the Kullback-Leibler best model (Burnham & Anderson 1998). This means that the analysis cannot confidentially distinguish between the two models to identify the best model in the competition.

Table 3-4: Results of the model competition using total abundance for the forest habitat study sites with a selection criterion. Null deviance of model is 1030.05 for 485 records. The dispersion parameter for the full model is approximately 1.23. The symbol “I” represents the intercept for the model. Other variable symbols are described in Table 3.2.

Analysis Description	Models	Residual Deviance	K	QAIC	QAIC_i – minimum QAIC	Akaike weights
Abundance ~ Habitat Area + Habitat in Landscape + Fragmentation + Interaction between Habitat Area and Habitat in Landscape Ab ~ Ar + La + F + Ar*La	I = -3.27*** Ar = 3.58 x 10 ⁻⁵ *** La = 5.37 x 10 ⁻⁶ *** F = 0.22*** Ar*La = -6.23 x 10 ⁻¹¹ ***	504.11	6	421.4	0	0.87
Abundance ~ Urban Area + Habitat Area Ab ~ Ar + Ur	I = -1.25*** Ar = 1.48 x 10 ⁻⁵ *** Ur = -2.03 x 10 ⁻⁶ ***	513.65	4	425.2	3.7	0.13
Abundance ~ Habitat Area + Habitat in Landscape + Interaction between Habitat Area and Habitat in Landscape Ab ~ Ar + La + Ar*La	I = -3.04*** Ar = 3.27 x 10 ⁻⁵ *** La = 4.95 x 10 ⁻⁶ *** Ar*La = -5.57 x 10 ⁻¹¹ ***	530.49	5	440.8	19.4	5.3 x 10 ⁻⁵
Abundance ~ Habitat Area + Floristics Ab ~ Ar + Fl	I = -1.62*** Ar = 1.61 x 10 ⁻⁵ *** Fl = -1.55*	591.4	4	488.3	66.9	2.6 x 10 ⁻¹⁵
Abundance ~ Habitat Area Ab ~ Ar	I = -1.73*** Ar = 1.65 x 10 ⁻⁵ ***	602.68	3	495.5	74.1	7.2 x 10 ⁻¹⁷
Abundance ~ Urban Area + Habitat in Landscape + Interaction between Urban Area and Habitat in Landscape Ab ~ Ur + La + F + Ur*La	I = -0.67** Ur = -2.18 x 10 ⁻⁶ * La = 2.11 x 10 ⁻⁶ ** F = 6.01 x 10 ⁻⁴ (NS) Ur:*La = -1.43 x 10 ⁻¹² (NS)	841.7	6	695.6	274.2	2.5 x 10 ⁻⁶⁰
Abundance ~ Urban Area Ab ~ Ur	I = -0.17(NS) Ur = -2.58 x 10 ⁻⁶ ***	868.14	3	711.1	289.7	1.1 x 10 ⁻⁶³

Significance codes: *** P<0.001; ** P<0.01; * P<0.05; • P<0.1 ^{NS} P>0.1

The third best model is clearly not within competition for the best model since its QAIC differs by almost 20 units from the minimum QAIC value. The model with the lowest QAIC (R ~ Ar + La + F + Ar*La) accounts for approximately 51% of the null deviance.

The relationship between the total abundance variable and the explanatory variables is the same as for the richness analysis. Habitat area, amount of habitat in the landscape and fragmentation are positively related to total abundance. The amount of urbanization in the landscape and the amount of exotic vegetation communities in the habitat patch (floristics variable) have a negative

relationship with total abundance. The interaction between habitat area and the amount of habitat in the landscape is significant and negatively related to total abundance. The interaction between the amount of urbanization in the landscape and the habitat in the landscape is not significant.

3.2 Testing all treed habitats

This test looked at all treed habitats including deciduous, mixed and coniferous forests, plantations, and deciduous, mixed and coniferous swamps.

3.2.1 Treed habitat with no selection criterion

No selection criterion was applied for the first analysis. The spatial test for independence found that there was a lack of independence. In fact, semivariograms showed significant autocorrelation at very short distances. Consequently, this analysis was abandoned.

3.2.2. Modelling species richness in treed habitats with a selection criterion

This analysis on all treed habitats with a selection criterion of 30 meters gave a database of 465 records after the removal of four visually identified outliers. The location of the study sites is shown in Figure 3-2.

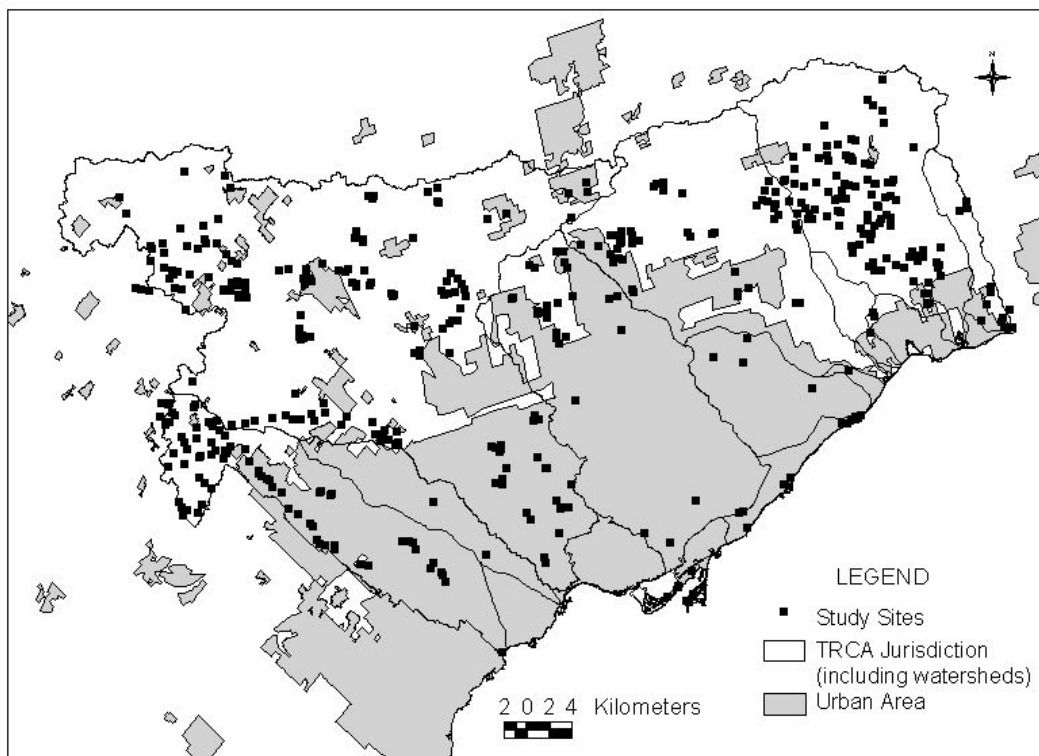


Figure 3-2: Location of treed habitat study sites.

The variables displayed in Table 3.5 were included in the analysis.

Table 3-5: Description of variables included in the all treed habitat analysis with a selection criterion.

Variable name	Symbol	Mean	Spread (Interquartile value)
Richness	R	0.27	0*
Abundance	Ab	0.42	0*
Habitat Area	Ar	33,610.8 m ²	31,850.2 m ²
Floristics	Fl	0.1	0 [†]
Habitat in Landscape	La	217,703.4 m ²	194,725.3 m ²
Urban Area	Ur	417,736.8 m ²	797,713.6 m ²
Fragmentation	F	8.36	5

[†] The zero spread for the floristics variable shows that most of the habitat patches are dominated by native habitat types. *See below for explanation.

Histograms of the variables are found in Appendix I. The zero spread for the response variables richness and total abundance results from the large number of habitat patches empty of any birds. A total of 71 patches out of the 465 have birds present. This proportion was still deemed sufficient to create the models, and the models did not show instability.

The first competition for the treed habitat also used species richness as the response variable. Table 3.6 shows the results from this analysis. As with the two previous model competitions, the value of the coefficient and its sign indicates the nature of the relationship between the explanatory and response variable.

Table 3-6: Results of the model competition using species richness for the treed habitat study sites with a selection criterion. The symbol “I” represents the intercept for the model. Other variable symbols are described in Table 3.5. The null deviance for the model is 521.24 with 465 records. The dispersion parameter is approximately 0.85.

Analysis Description	Models	Residual Deviance	K	QAIC	QAIC_i - minimum QAIC	Akaike weights
Richness ~ Urban Area + Habitat Area R ~ Ar + Ur	I = -2.03*** Ar = 1.61x 10 ^{-5***} Ur = -1.30 x 10 ^{-6***}	295.65	4	355.1	0	0.98
Richness ~ Habitat Area + Floristics R ~ Ar + Fl	I = -2.18*** Ar = 1.63 x 10 ^{-5***} Fl = -8.73*	302.70	4	363.4	8.3	1.6 x 10 ⁻²
Richness ~ Habitat Area + Habitat in Landscape + Interaction between Habitat Area and Habitat in Landscape R ~ Ar + La + Ar*La	I = -2.94*** Ar = 1.83 x 10 ^{-5***} La = 2.02 x 10 ^{-6***} Ar*La = -6.11 x 10 ^{-12(NS)}	310.29	5	374.3	19.2	6.7 x 10 ⁻⁵
Richness ~ Habitat Area + Habitat in Landscape + Fragmentation + Interaction between Habitat Area and Habitat in Landscape R ~ Ar + La + F + Ar*La	I = -2.96*** Ar = 1.87 x 10 ^{-5***} La = 2.05 x 10 ^{-6**} F = 1.49 x 10 ^{-2(NS)} Ar*La = -5.99 x 10 ^{-12(NS)}	309.67	6	375.6	20.5	3.5 x 10 ⁻⁵
Richness ~ Habitat Area R ~ Ar	I = -2.36*** Ar = 1.68 x 10 ^{-5***}	323.79	3	386.2	31.0	1.8 x 10 ⁻⁷
Richness ~ Urban Area + Habitat in Landscape + Interaction between Urban Area and Habitat in Landscape R ~ Ur + La + F + Ur*La	I = -1.38*** Ur = -2.45 x 10 ^{-6**} La = 8.44 x 10 ^{-7(NS)} F = -6.80 x 10 ^{-2*} Ur:*La = 5.19 x 10 ^{-12*}	443.66	6	532.9	177.8	2.4 x 10 ⁻³⁹
Richness ~ Urban Area R ~ Ur	I = -1.0*** Ur = -1.40 x 10 ^{-6**}	480.30	3	570.0	214.8	2.2 x 10 ⁻⁴⁷

Significance codes: *** P<0.001; ** P<0.01; * P<0.05; • P<0.1; ^{NS} P>0.1

The model containing habitat area and the amount of urbanization within the landscape is the best Kullback-Leibler model with the lowest QAIC of 355.1. Strong evidence for this statement is found in its Akaike weight of 0.98. This model explains 57% of the null deviance. The second best model includes habitat area and the floristics variable describing the proportion of exotic vegetation communities in the habitat patch. This model has weak support as the best model because its QAIC value differs from the minimum QAIC by approximately 8 units (Burnham & Anderson 1998).

Habitat area and the amount of habitat in the landscape are positively related to species richness. The amount of urbanization in the landscape and the amount of exotic vegetation communities in the habitat patch (floristics variable) has a negative relationship with species richness. Interestingly, the fragmentation variable has both a positive and a negative sign in different

models. When it is included in the model with habitat area and amount of habitat in the landscape it is positive, and when it is included in a model with urbanization and habitat in the landscape it is negative. However, the variable is only significant in the models where it is negative.

The interaction between habitat area and the amount of habitat in the landscape is negative but not significant in the two models in which it is included. The interaction between the amount of urbanization in the landscape and the habitat in the landscape is significant and positive.

3.2.3 Modelling total abundance in treed habitats with a selection criterion

The analysis using total abundance as the response variable used the same dataset as the immediately preceding analysis. Therefore, 465 records were also included after outliers were removed. The best model in this analysis once again included habitat area and the amount of urbanization in the landscape with a QAIC value of 403.7. This model explains approximately 49% of the null deviance. Its Akaike weight of 0.96 gives strong evidence that this is the best Kullback-Leibler model of the models considered. As with the preceding model competition, the second best model includes habitat area and floristics variables. It had a QAIC value of 410.3, which differed by approximately 7 units; this gives only weak evidence that this is the best model in this competition. Therefore, the first model with urbanization and habitat area can be considered the best model.

Table 3-7: Results of the model competition using total abundance for the treed habitat study sites with a selection criterion. Null deviance is 841.73 with 465 records. The symbol “I” represents the intercept for the model. Other variable symbols are described in Table 3.5. The dispersion parameter is approximately 1.05.

Analysis Description	Models	Residual Deviance	K	QAIC	QAIC_i - minimum QAIC	Akaike weights
Abundance ~ Urban Area + Habitat Area Ab ~ Ar + Ur	I = -1.82*** Ar = 1.77 x 10 ⁻⁵ *** Ur = -1.35 x 10 ⁻⁶ ***	415.40	4	403.7	0	0.96
Abundance ~ Habitat Area + Floristics Ab ~ Ar + Fl	I = -1.97*** Ar = 1.79 x 10 ⁻⁵ *** Fl = -12.7*	422.25	4	410.3	6.5	3.7 x 10 ⁻²
Abundance ~ Habitat Area + Habitat in Landscape + Fragmentation + Interaction between Habitat Area and Habitat in Landscape Ab ~ Ar + La + F + Ar*La	I = -2.82*** Ar = 2.17 x 10 ⁻⁵ *** La = 2.15 x 10 ⁻⁶ *** F = 2.89 x 10 ⁻² (NS) Ar*La = -8.65 x 10 ⁻¹² (NS)	436.32	6	427.7	24.0	6.1 x 10 ⁻⁶
Abundance ~ Habitat Area + Habitat in Landscape + Interaction between Habitat Area and Habitat in Landscape Ab ~ Ar + La + Ar*La	I = -2.76*** Ar = 2.09 x 10 ⁻⁵ *** La = 2.10 x 10 ⁻⁶ *** Ar*La = -8.81 x 10 ⁻¹² (^o)	439.66	5	428.8	25.1	3.4 x 10 ⁻⁶
Abundance ~ Habitat Area Ab ~ Ar	I = -2.16*** Ar = 1.84 x 10 ⁻⁵ ***	455.98	3	440.4	36.7	1.1 x 10 ⁻⁸
Abundance ~ Urban Area + Habitat in Landscape + Interaction between Urban Area and Habitat in Landscape Ab ~ Ur + La + F + Ur*La	I = -0.94*** Ur = -2.68 x 10 ⁻⁶ ** La = 7.06 x 10 ⁻⁷ (NS) F = -7.32 x 10 ⁻² * Ur*La = 5.69 x 10 ⁻¹² *	721.63	6	699.5	295.7	5.9 x 10 ⁻⁶⁷
Abundance ~ Urban Area Ab ~ Ur	I = -0.62*** Ur = -1.46 x 10 ⁻⁶ **	778.14	3	747.3	343.6	2.4 x 10 ⁻⁷⁵

Significance codes: *** P<0.001; ** P<0.01; * P<0.05; • P<0.1 ^{NS} P>0.1

Habitat area and the amount of habitat in the landscape are positively related to total abundance. The amount of urbanization in the landscape and the amount of exotic vegetation communities in the habitat patch (floristics variable) have a negative relationship with species total abundance. As with the preceding analysis, the fragmentation variable is both positive and negative in different models, although it is only negative when it is a significant parameter in the model. The interaction between habitat area and the amount of habitat in the landscape is again not significant (at $P \leq 0.05$ criterion) and negatively related to total abundance. The interaction between the amount of habitat in the landscape and urbanization is significant and positive.

3.3 Testing assumptions

The comparison of study sites assumed that richness and total abundance were not affected by the specific observer or the year it was surveyed. The effect of the year was of particular concern since bird populations can change from year to year (Odell & Knight 2001). Each site was typically not surveyed on consecutive years and sites compared with each other could be surveyed on different years.

To test this assumption, observer and year were coded as factor variables. Each observer was given a numerical code and each year that a patch was surveyed was given the four digit year as a code. These data were only available for patches in which birds were found since the variables were associated with the species point data. To test the importance of the observer and year, they were entered as factors in a Poisson model containing combinations of the other relevant variables. This analysis was completed for both the treed habitats and the forest habitats for the richness response variable. For the forest habitat analysis, four outliers were identified visually and removed. The model was then tested using an analysis of variance (ANOVA) and an F-test. Since this information was only available for patches containing focal species, a model competition analysis was not appropriate. Table 3.8 shows the results of a number of ANOVA explorations for the forest habitat analysis.

Table 3-8: ANOVA test for observer and date variables in forest habitat analysis. Significance codes shown below for F-test.

Model	F test value	P value and significance
Richness ~ Observer + Date	Observer: 1.4 Date: 2.0	P = 0.18 ^(NS) P = 0.10 ^(NS)
Richness ~ Observer + Date + Habitat Area + Urban Area	Observer: 1.7 Date: 2.4 Habitat Area: 18.3 Urban Area: 0.05	P = 0.08 ^(•) P = 0.06 ^(•) P = 5.6 x 10 ⁻⁵ *** P = 0.83 ^(NS)
Richness ~ Habitat Area + Urban Area + Observer + Date	Habitat Area: 18.7 Urban Area: 1.0 Observer: 2.0 Date: 1.2	P = 4.6 x 10 ⁻⁵ *** P = 0.33 ^(NS) P = 0.03* P = 0.3 ^(NS)

Significance codes: *** P<0.001; ** P<0.01; * P<0.05; • P<0.1; ^{NS} P>0.1

The ANOVA analysis for the generalized linear model tests “the reductions in the residual deviance as each term of the formula is added” (from information on ANOVA for generalized linear models, R Development Core Team 2004). Therefore, the order in which variables are added to the models affects their significance levels. The most conservative test of observer and year was tested with these variables added first in the model. The next test determined the significance of the observer and year variables after the addition of the habitat area and urban area variables.

A similar test was carried out for the treed habitat analysis (Table 3-9).

Table 3-9: ANOVA test for observer and date variables in treed habitat analysis. Significance codes shown below for F-test.

Model	F test value	P value and significance
Richness ~ Observer + Date	Observer: 1.2 Date: 1.3	P = 0.30 ^(NS) P = 0.28 ^(NS)
Richness ~ Observer + Date + Habitat Area + Urban Area	Observer: 2.2 Date: 2.4 Habitat Area: 37.5 Urban Area: 2.1	P = 0.034* P = 0.08 ^(•) P = 1.2 x 10 ⁻⁷ *** P = 0.15 ^(NS)
Richness ~ Habitat Area + Urban Area + Observer + Date	Habitat Area: 47.6 Urban Area: 4.6 Observer: 1.2 Date: 1.3	P = 7.1 x 10 ⁻⁹ *** P = 0.04* P = 0.32 ^(NS) P = 0.28 ^(NS)

Significance codes: *** P<0.001; ** P<0.01; * P<0.05; • P<0.1; ^{NS} P>0.1

It is not surprising that these variables have some significant explanatory effect in the models. Observer is significant when entered as the first variable with habitat area and urban area in the treed analysis. This may show that different observers have a bias in detecting different levels of species richness. However, the significant effect of observer could have another explanation. It could simply show that certain observers work in areas of higher species richness. The analysis also shows that the observer effect is not significant after the habitat area variable is entered for the treed habitat analysis. Interestingly, observer is only significant when it preceded the habitat and urban variables in the forest analysis.

The effects of the observer on the model competition conclusions are difficult to discern. The tested observer bias here shows that observers has a relationship with the level of species richness detected, but we do not know if the observers affected the ability to detect any birds since this cannot be tested on the complete database (e.g. the observer data was unavailable for patches without birds). For this analysis, the effect of the observer would be most important if the differences in detection were consistent with changes in the other variables such as urbanization. For example, if observers detected native birds less frequently in urban habitat patches than in non-urban areas, this could be an alternative explanation for the importance of the urban variable. This is unlikely since the urbanization is found throughout most to the study area and observers are not usually restricted to urban or non-urban areas. Further exploration of the database found that the observers were not clearly associated with the urban area. The observer bias should be noted as a factor possibly biasing the detection of different levels of richness.

Date does not appear to be important in either the treed or forest habitat analysis. Further exploration of the database revealed that the majority of the bird records were found in two years

(2002 and 2003). The lack of a relationship between date and richness is perhaps due to this lack of spread.

The landscape size was deemed appropriate for the final list of species included in the analysis (Table 3.1). The following table shows that literature findings for all the species for their territoriality and territory size. As mentioned in Section 2.2.2, the landscape size was chosen to be larger than the territory size and to encompass day-to-day individual dispersal of birds. The chosen landscape size of 800 m (approximately 201 ha) is still deemed appropriate based on the species information.

Table 3-10: Territory information for species included in analyses.

Common Name	Species	Habitat	Description of Territoriality	Reported Territory Size	Source
American redstart	<i>Setophaga ruticilla</i>	Mature deciduous forest, but also mixed forests, successional woodlands.	Territorial	Generally less than 0.1 ha, but may be larger	(Sherry & Holmes 1997)
American woodcock	<i>Scolopax minor</i>	Nests in a variety of forests with openings.	Females not strongly territorial when breeding		(Keppie 1994)
Cooper's hawk	<i>Accipiter cooperii</i>	In deciduous, mixed and evergreen forests	Little information	distance between nests 0.7-1.0 km	(Rosenfield & Bielefeldt 1993)
black-and-white warbler	<i>Mniotilta varia</i>	Woodlands, second growth forests and mature forests.	Territorial	0.9-6.6 ha in Alberta	(Kricher 1995)
black-throated blue warbler	<i>Dendroica caerulescens</i>	In hardwood and mixed forests.	Territorial	1-4 ha	(Holmes 1994)
black-throated green warbler	<i>Dendroica virens</i>	Coniferous forest, mixed forests and occasionally deciduous forests	Strongly territorial	0.3-0.9 ha in western Ontario	(Morse 1993)
brown creeper	<i>Certhia americana</i>	Found in a variety of forests	Territorial	2.3-6.4 ha in Michigan	(Heji et al. 2002b)
golden-crowned kinglet	<i>Regulus satrapa</i>	Breeds in a variety of woodlands as well as plantations and swamps.	Territorial	Averages 1.6 ha;	(Ingold 1997)
hermit thrush	<i>Catharus guttatus</i>	Uses a broad spectrum of forest habitat, both wet and dry habitats.	Territorial	Algonquin Provincial Park, Ontario average size was 0.722 ha	(Jones & Donovan 1996)

northern waterthrush	<i>Seiurus noveboracensis</i>	Breeds in wooded swamps, thickets and mixed and deciduous woods.	Territorial	0.8-1.5 ha as one example of range	(Eaton 1995)
ovenbird	<i>Seiurus aurocapillus</i>	In deciduous and mixed forests, but also can be in coniferous forests.	Territorial	Size usually inverse to food supply (0.61-1.6 ha in Ontario)	(Van Horn & Donovan 1994)
pileated woodpecker	<i>Dryocopus pileatus</i>	Deciduous and coniferous forests	Territory defended all year.	Not given.	(Bull & Jackson 1995)
pine warbler	<i>Dendroica pinus</i>	Breeds in upland pine forests and mixed forests. Will breed in deciduous forests if pine is present.	Territorial	Little information on size of territory (average of 1.0 ha in Minnesota)	(Rodewald et al. 1999)
ruffed grouse	<i>Bonasa umbellus</i>	Most abundant in early successional forests.	Only males territorial	averaged 2.1 ha in Alberta and Wisconsin	(Rusch et al. 2000)
scarlet tanager	<i>Piranga olivacea</i>	Prefers mature deciduous woods, but also in mixed forests, successional woodlands and plantations.	Territorial. Size varies with habitat.	0.9-1.2 ha and 2.5-5.0 ha	(Mowbray 1999)
sharp-shinned hawk	<i>Accipiter striatus</i>	Breeds in stands of deciduous, mixed and coniferous forests	Highly territorial while breeding	1.2 km mean distance between nests in New Brunswick	(Bildstein & Meyer 2000)
veery	<i>Catharus fuscescens</i>	Strong preference for riparian areas, but also deciduous forests, and mixed forests	Territorial mostly around nest	0.1-2.0 ha in Ontario	(Moskoff 1995)
winter wren	<i>Troglodytes troglodytes</i>	Associated with moist forests, mostly coniferous.	Territorial	Size differs with habitat and topography	(Heji et al. 2002a)
wood thrush	<i>Hylocichla mustelina</i>	Uses a wide variety of deciduous and mixed forests.	Territorial	0.08-2.8 ha	(Roth et al. 1996)
yellow-rumped warbler	<i>Dendroica coronata</i>	Breeds in coniferous forests, mixed forests and less common in deciduous forests.	Territorial	0.45-0.8 ha	(Hunt & Flaspohler 1998)

4.0 Discussion of Findings

The four model competitions show that, from the set of models considered, the model containing habitat area and the amount of urbanization within the landscape is the best model overall. In three out of the four competitions this model is the best Kullback-Leibler information model. In the fourth competition, it is considered as strong as the model containing the habitat area variable and the landscape variables. In the treed habitat analysis, the model with habitat area and floristics only has weak evidence as a co-competing model. This supports my third hypothesis from the literature review: habitat area is the most important variable, but landscape variables are also important. The urbanization variable is the most important landscape variable.

Consistent with the literature, the model competition demonstrated that habitat area is an important variable to account for native avian species diversity. It is present in all of the highest ranking models. In all four model competitions, the area variable is present in the first five models ranked according to QAIC value. Furthermore, models without the habitat area variable consistently describe very little of the variance of the data. For example, in the forest habitat competition, the model without the habitat area variable ($R \sim Ur$) ranks the lowest in the model competition.

Although the habitat area variable is important, it cannot sufficiently explain the data by itself. The models with just habitat area ($R \sim Ar$ or $Ab \sim Ar$) do not compete with the best model in each of the four model competitions. In all four model competition exercises, the model with just the habitat area variable is fifth of the seven models. This model ranks lower than the models containing the habitat area variable accompanied by either landscape variables or the floristics variable. This also indicates that landscape variables are important for explaining bird species richness or total abundance.

The results from the four model competitions also indicate that urbanization is an important factor. In three of the competitions, the model containing just habitat area and urban area ($R \sim Ar + Ur$) is the best model in the competition; it accounts for more of the data's variance than the other models containing habitat area and the other landscape variables (e.g. $R \sim Ar + La + F$). The urbanization variable is consistently significant, and it is negatively related to both species richness and abundance. The inclusion of the urbanization variable in the best overall model also indicates that matrix characteristics are important for native bird species diversity. The type of matrix seems to be an important factor along with the size of the habitat patch. This is consistent with Friesen's (1998) assertion that the impact of urbanization was "only slightly less extreme than the removal of forests altogether."

The overall results from the four model competition exercises supports the hypothesis that landscape variables must be considered with habitat area. This best overall model ($R \sim Ar + Ur$) represents the habitat area and a matrix characteristic. The relative importance of the other landscape variables (amount of habitat in the landscape and fragmentation) is difficult to discern.

For the forest habitat model competitions, the model containing habitat area, habitat in the landscape, and fragmentation ($Ab \sim Ar + La + F + Ar*La$) is as strong as the model with habitat area and urban area ($Ab \sim Ar + Ur$). However, in the treed habitat model competitions, the second model in the hierarchy, which has weak evidence as the best model, contains the habitat area and floristics variables, both variables describing the habitat patch. From the model competition, it can be asserted that matrix characteristics cannot be ignored, but other landscape habitat variables may not always be strong factors accounting for avian diversity. Some authors have hypothesized that the habitat in the landscape would become more important to birds in urban areas (Berry & Bock 1998) and certain theories such as island biogeography and metapopulation state that adjacent habitat is very important (MacArthur & Wilson 1967). In my study, landscape habitat variables are surprisingly less important than the landscape urbanization variable.

Since the habitat in the landscape and fragmentation seem to be less important landscape variables than urbanization, one could argue that these results support suggestions that metapopulation models are less appropriate for birds (Esler 2000). It may be that a rescue effect, as explained in metapopulation models, is less important in the fragmented landscapes adjacent to urban areas. As well, adjacent habitat may not be perceived as supplementing individual territories for the small patches studied in this project. However, answers to these questions can only be discerned through further investigation.

The literature alludes to the greater relative importance of habitat in the landscape than fragmentation for native birds. This model competition could not discern this relative difference in importance. In the forest habitat analysis, the fragmentation variable is not significant for two of the three models. However, in the treed habitat analysis, it is significant in two of the three models. The habitat in the landscape variable is also inconsistently significant. Since both variables are inconsistently significant, this analysis can not compare their relative importance.

The importance of the vegetation variable in the treed habitat model competitions indicates that native birds may be negatively affected by, or they may avoid vegetation communities dominated by non-native species. Other studies have alluded to this relationship (Beissinger & Osborne 1982). In the treed analysis, the habitat area and floristics model ($R \sim Ar + Fl$) has weak evidence as the best model with the habitat area and urbanization model ($R \sim Ar + Ur$). This gives a further indication that patch characteristics are very important in relation to bird species diversity and distribution. It is important to note, however, that this model competition indicates that the effect of urbanization is more important than the effect of non-native vegetation. If the effect of urbanization is fully explained by the differences in vegetation structure found in the urban area, as it was operationalized here in terms of native versus non-native vegetation, then it would be expected that the models containing the vegetation variable could be considered the best. This is not the case.

There are some hypotheses that attempt to explain the important negative effect of urbanization on native bird species diversity in habitat patches. Research has yet to discern if the influence of urbanization is behavioural or if it has an effect on mortality. Birds may preferentially choose territories away from urban areas or disturbances near urban areas may decrease population sizes. Some disturbances associated with urban areas have been studied for their effects on avian populations. Domestic predators, which are strongly associated with urban housing density (Odell & Knight 2001), may cause serious avian mortality. Urbanization may bring other adjacent disturbances such as pollution and human-use degradation. There is some evidence that brown-headed cowbird brood parasites may be more prevalent in fragmented landscapes (Rodewald & Yahner 2001). The three most prevalent species in the databases considered – ovenbird, wood thrush and scarlet tanager - are all susceptible to brown-headed cowbird parasitism (Mowbray 1999; Roth et al. 1996; Van Horn & Donovan 1994). Some research has indicated a significant difference in nest predation rates between suburban and rural areas (with suburban rates being higher)(Wilcove 1985), while other studies have not supported this finding for predators or brood parasites (Danielson et al. 1997; Melampy et al. 1999). Even if increased parasitism or predation occurs, it may not have an effect on the native bird populations (e.g. Phillips et al. 2005). Further investigation needs to understand the cause of the negative influence of urbanization on avian diversity.

As stated earlier, the relative importance of the habitat area variable found in my study is expected given the abundance of literature correlating bird richness and abundance to habitat area. The relative importance of the urbanization variable is perhaps less expected or, at least, as stated in the introduction, it is an uncommon result because landscape studies are rarely situated in or adjacent to urban areas. One could argue that the small patches prevalent within my study area may be more susceptible to the influences of factors within the matrix, especially urbanization (Forman & Godron 1986). However, the findings from this analysis demonstrate that these effects of the urbanized matrix are not solely due to the effect of habitat size. My analysis shows that matrix characteristics are important for native birds in the Greater Toronto Area and the effects of urbanization cannot be ignored.

4.1 Further explanation of results

There are differences in the relative model hierarchy between the forest habitat and the treed habitat. The model with the vegetation variable is the second best model in the treed analyses ($R \sim Ar + Fl$) while the model with habitat area and the other landscape variables ($R \sim Ar + La + F + Ar*La$) is the second best model in the forest habitat analysis. In the treed habitat, more exotic species dominated vegetation communities are present (since plantations are often dominated by exotic species), while forests and treed wetlands tend to have fewer exotic vegetation communities. Therefore, the floristics variable may be better at explaining vegetation differences at the patch level

for the treed habitat analysis since there is more variation between the diverse vegetation communities included in this analysis. For the forest analysis, the lower variability of the floristics variable indicates that this variable may not adequately explain differences in vegetation, but this also may reflect the relative similarity between forest habitats as opposed to the varied treed habitats. Another explanation could be related to the smaller number of patches with the focal birds present in the treed habitat analysis.

4.2 Further exploration of best model overall

Modelling empirical data has the potential to serve a predictive capacity that may be particularly useful for conservation planning. I further explored the best model ($R \sim A_r + U_r$) in both the forest and treed habitat analysis by inserting raw data for both variables to determine their relative influence on species richness. This sensitivity analysis shows that, for both analyses, urban area has a greater effect on species richness. Table 4-1 shows the findings. For each analysis, approximately 10% of the data points were entered into the model and the average change in species richness was determined for a 10% increase in both habitat area and urban area.

Table 4-1: Sensitivity analysis for best model overall.

Analysis Type	Change in variable	Resulting change in species richness (approximated and averaged)
Forest habitat	10% increase in habitat area	10% increase
	10% increase in urban area	20% decrease
Treed habitat	10% increase in habitat area	13% increase
	10% increase in urban area	24% decrease

The sensitivity analysis shows that the urban area variable has a greater effect on species richness than the habitat area variable. This is interesting since in the model competition, urban area alone explained much less of the variance of the data than the habitat area variable. It is important to note that these results should be applied with caution since the best model still only explains approximately 50% of the variation in the data.

4.3 Interaction terms

A few interactions were included in the model competitions. The interactions mean that the effect of one variable depends on the value of the other variable (ter Braak & Looman 1995). They show complex relationships between some of the variables, particularly the significant interactions between habitat area and habitat in the landscape ($Ar*La$) and between urban area and habitat in the landscape ($Ur*La$).

The interaction between habitat area and habitat in the landscape was inconsistently significant, but always negative. One interpretation of this interaction could be that an increase in the habitat in the landscape decreases the effect of habitat area; conversely, an increase in habitat area may decrease the effect of habitat in the landscape. Mathematical exploration of the interaction term shows that the interaction with the habitat in the landscape variable roughly halves the value for the habitat area variable in the equation.

The interaction between habitat in the landscape and urbanization was significant for the treed habitat analysis. This can be similarly interpreted. The positive sign of this interaction could mean that the habitat in the landscape may lessen the negative effect of urbanization. The infrequent significance of this interaction in the four analyses may indicate that this is an unimportant interaction effect. Mathematical exploration of this interaction for the treed habitat data showed that the habitat in the landscape variable decreases the value for urban area in the equation by roughly half.

Although the interactions appear to be mathematically important, it is difficult to ascertain their biological significance. This interrelationship between the variables is not surprising in terms of their effect on diversity since individuals likely respond to aspects of the landscape simultaneously (Collinge 1996). Furthermore, these variables are likely influenced by the same landscape processes, such as historical land clearing for agriculture, which may cause these landscape elements to be interrelated. It is interesting to note that the complex relationship between habitat area and amount of habitat in the landscape has been integrated into woodland conservation recommendations in Ontario. The Ontario Ministry of Natural Resources has recommended the designation of significant woodlands for those areas greater than 2 ha in size in landscapes with less than five percent woodland cover; a larger size cut-off is recommended for landscapes with greater woodland cover (Larson et al. 1999).

4.4 Implications for planning and conservation in Ontario

Ontario has a commitment to protecting natural heritage. For example, planning tools such as the Provincial Policy Statement explicitly recommend actions applicable to the provincial

Planning Act for the protection of natural heritage such as species biodiversity (Ministry of Municipal Affairs and Housing 2005). Another important piece of legislation for conservation of biodiversity in terms of urban development is the Oak Ridges Moraine Conservation Act (Ministry of Municipal Affairs and Housing 2002). It plans for areas within and adjacent to the Greater Toronto Area for the preservation of various natural resources and sustained human use of the land. My research findings have implications for these planning documents.

The model competition exercise employed here compared the relative importance of a variety of variables referring to the landscape and patch qualities of a habitat patch for modelling native avian diversity. The best overall model included habitat area and urbanization within the landscape. This indicates that the effects of both of these variables cannot be ignored for the planning and management of native bird communities in the Greater Toronto Area. As a result, planning and management tools should take these findings into account within the larger context of conservation of natural heritage and for wider planning goals for healthy and vibrant communities (Fraser 2003).

The findings of my research can be extended to a more general consideration of adjacent land-use and habitat patch characteristics for preservation of biodiversity. Ontario's Provincial Policy Statement (Ministry of Municipal Affairs and Housing 2005) sets out policy guidelines as applied to the Planning Act for a number of social goals, one of which is the maintenance of natural heritage resources (section 2.1 of the Provincial Policy Statement). Employing vague language, the policy insists on the protection of natural heritage features (including significant woodlands and territories of endangered and threatened species). Development in adjacent lands is not permitted unless the "ecological function of the adjacent lands have been evaluated and it has been demonstrated that there will be no negative impacts on the natural features or their ecological functions" (Ministry of Municipal Affairs and Housing 2005). The results from this model competition exercise indicate that urban development adjacent to maintained habitat can negatively affect native bird species. It appears that for maintaining native bird biodiversity in the Greater Toronto Area efforts should focus on preserving and possibly increasing habitat area, and, for areas deemed important by society to preserve avian biodiversity, urban development on adjacent lands should be considered a significant negative effect. To take into account this negative effect of urbanization, the policy statement could define urbanization as an important negative effect to be avoided in the adjacent lands of areas of significance, particularly for the conservation of native birds.

My findings are consistent with more recent legislation in Ontario such as the Oak Ridges Moraine Conservation Act (Ministry of Municipal Affairs and Housing 2002) in that natural features designated for protection have strong regulation for the types of adjacent land-use. For example, substantial residential development is largely restricted to areas designated as "countryside area" and "settlement areas" while focusing development away from natural heritage "core" and "linkage"

areas. Since adjacent land use is considered in this legislation, the intentions to enhance existing natural features should focus on increasing habitat areas for the conservation of native bird richness and abundance.

4.4.1 Implications for urban forestry and restoration

My findings also have implications for restoration, especially of urban forests. If the goal of an urban restoration project is to enhance native avian biodiversity, then the findings from this research cautions that the adjacent urban land use will have a negative impact on the richness and abundance. Increasing habitat area may not be able to compensate for this negative effect. This understanding of adjacent land use is already found in the restoration literature. For example, a restoration handbook for the Toronto area cautions that restoration site selection should take into account the adjacent land use:

“Although there may be similar habitat in several landscapes, they may function differently. In urban areas, the habitat will be subjected to stresses by humans, pets, and introduced plant species and will likely only support very common plants and animals” (Hough Woodland Naylor Dance Limited & Gore & Storrie Limited 1995).

My research findings of the negative effects of urban land use support this statement. Further research focusing on the effect of urbanization can assist large-scale restoration efforts to efficiently target the areas that will likely be most successful for their biodiversity enhancement goals for all species.

The importance of habitat area found in my results emphasizes the ecological restoration goal to increase the size of natural areas. For avian diversity, restoration projects on treed habitats should focus on increasing habitat area for bird species diversity, especially if this is a primary target species group for the project.

4.5 Recommendations for further research

Several interesting areas of study are suggested by my research findings. My simplest suggestion would be to expand optimization of landscape pattern studies in urban areas in other geographical locations with other focal species. In particular, it would be interesting to see the results of a similar model competition for non-migratory species such as small mammals. This may assist with understanding the relative importance of habitat landscape variables for species that may be more likely to form classic metapopulation structures.

Specific to native birds, it is important to understand the mechanisms behind the strong, predictive capacity of the urbanization variable. In particular, is urbanization an important factor in terms of a mortality risk or is urbanization avoided during habitat selection? Also, further work on

urbanization could attempt to understand if different patterns of urbanization affect species diversity such as local housing development patterns (e.g. Theobald et al. 1997). It would also be interesting to clarify the maximum distance at which urbanization in the landscape significantly affects species. This could assist further urban planning in its attempts to plan effectively for human and natural communities.

Appendix I: Descriptions of variables

Forest Habitat Variable Histograms

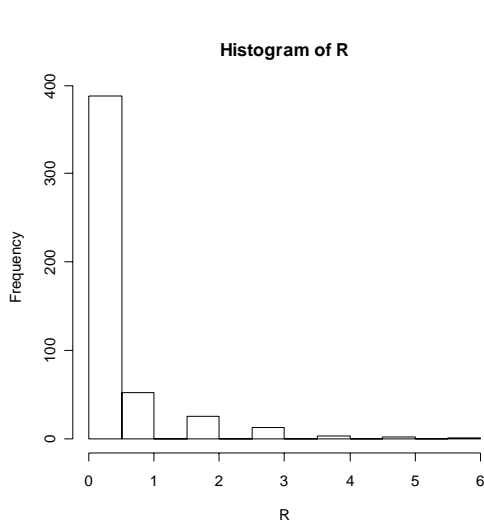


Figure I-1: Histogram of richness variable for forest habitat analysis.

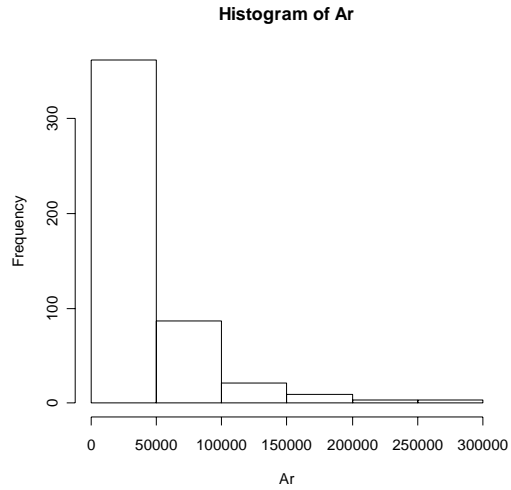


Figure I-3: Histogram of habitat area variable for forest habitat analysis.

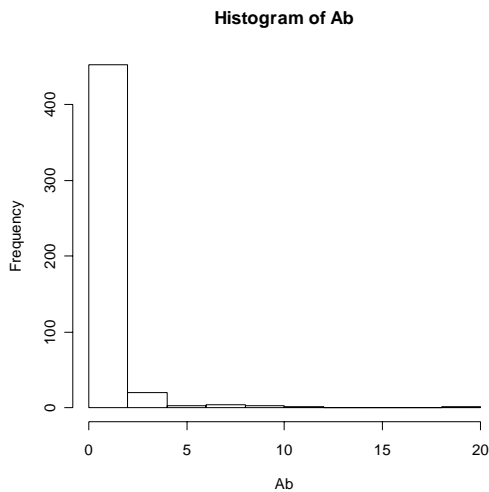


Figure I-2: Histogram of total abundance variable for forest habitat analysis.

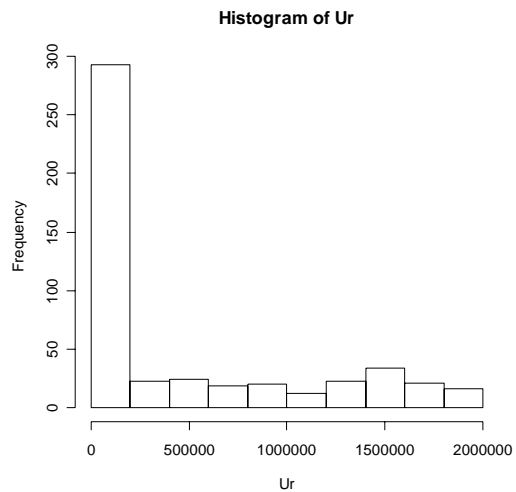


Figure I-4: Histogram of area of urbanization in the landscape variable in forest habitat analysis.

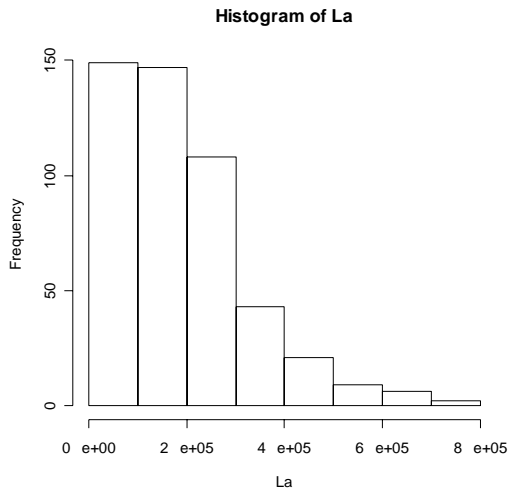


Figure I-5: Histogram of habitat in landscape variable in forest habitat analysis.

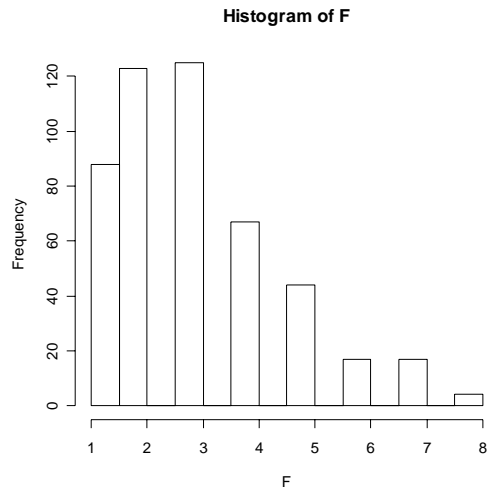


Figure I-7: Histogram of fragmentation variable in forest habitat analysis.

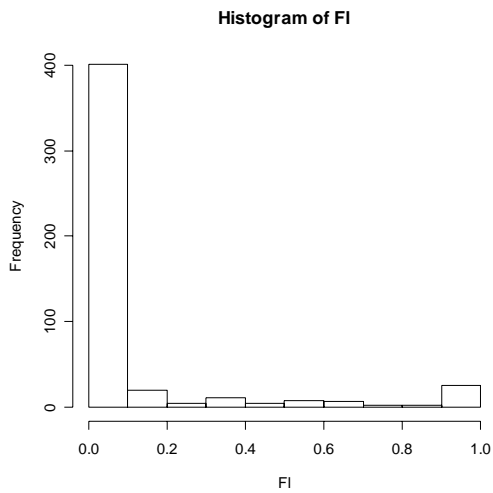


Figure I-6: Histogram of floristics variable showing the percent of non-native species dominated vegetation communities in focus patch for forest habitat analysis.

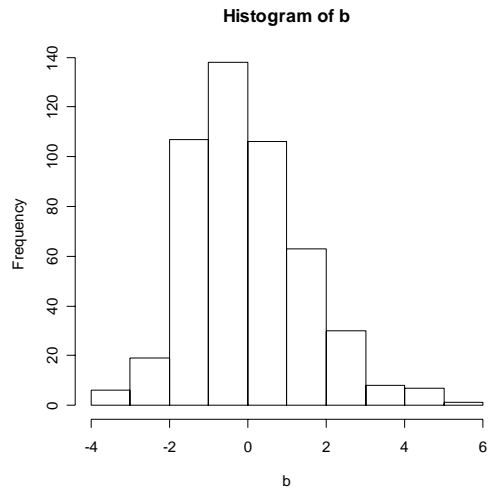


Figure I-8: Histogram of residuals of regression between fragmentation variable and habitat in landscape in forest habitat analysis. This variable was used in the analysis for the fragmentation variable.

Treed Habitat Analysis Variable Histograms

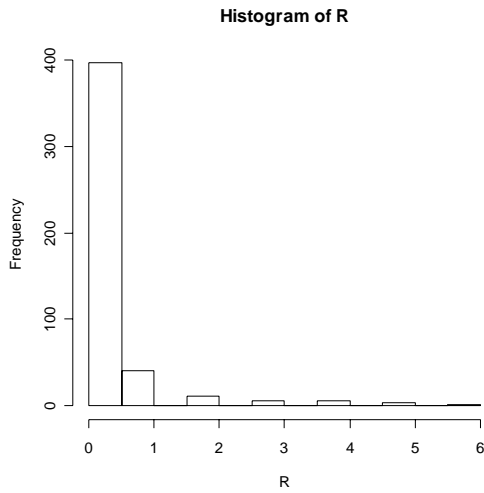


Figure I-9 Histogram of richness variable in treed habitat analysis.

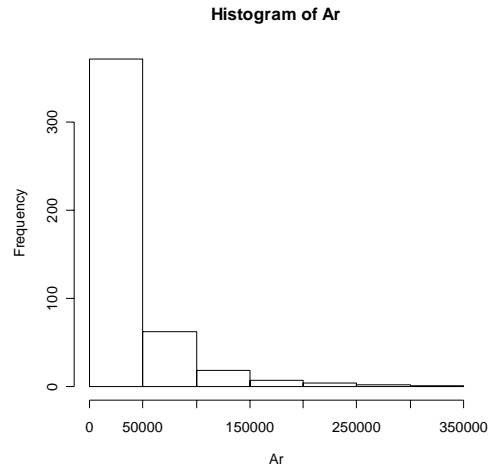


Figure I-11: Histogram of habitat area variable in treed habitat analysis.

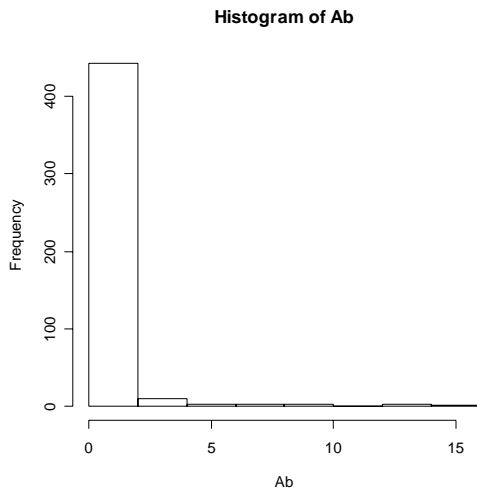


Figure I-10: Histogram of total abundance variable in treed habitat analysis.

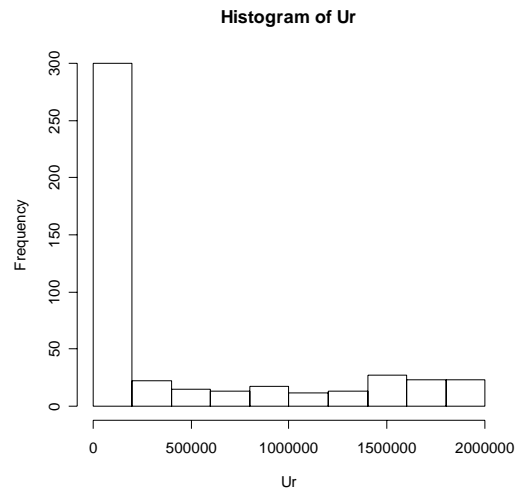


Figure I-12: Histogram of area of urbanization in the landscape variable in treed habitat analysis.

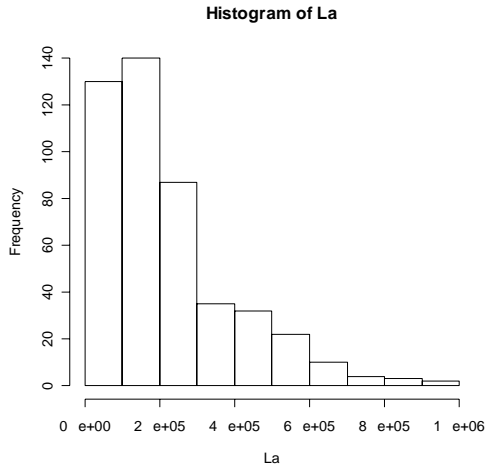


Figure I-13: Histogram of habitat in landscape variable in treed habitat analysis.

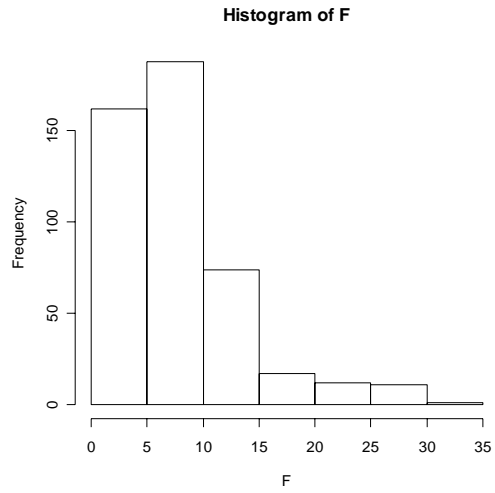


Figure I-15: Histogram of fragmentation variable in treed habitat analysis.

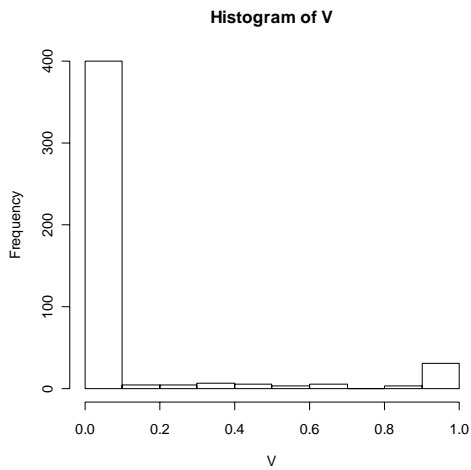


Figure I-14: Histogram of floristics variable showing the percent of non-native species dominated vegetation communities in focus patch for treed habitat analysis.

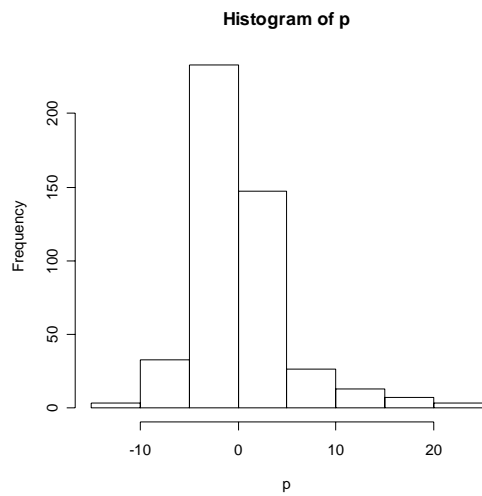
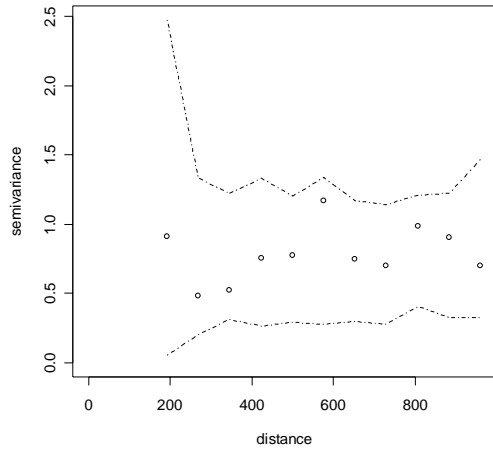


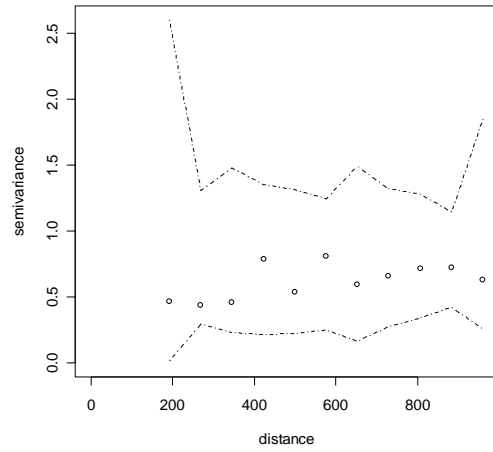
Figure I-16: Histogram of residuals of regression between fragmentation variable and habitat in landscape in treed habitat analysis. This variable was used in the analysis for the fragmentation variable.

Appendix II: Semivariograms of residuals for all models in analyses

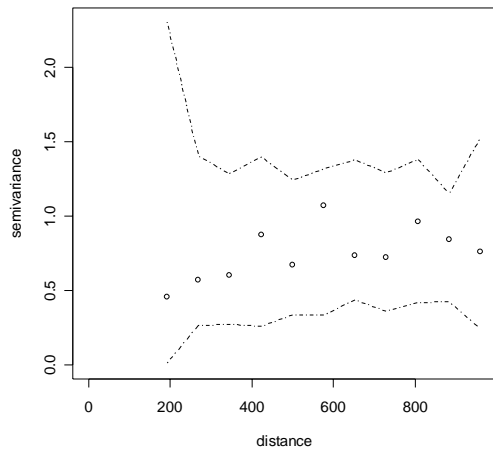
Forest habitat analysis



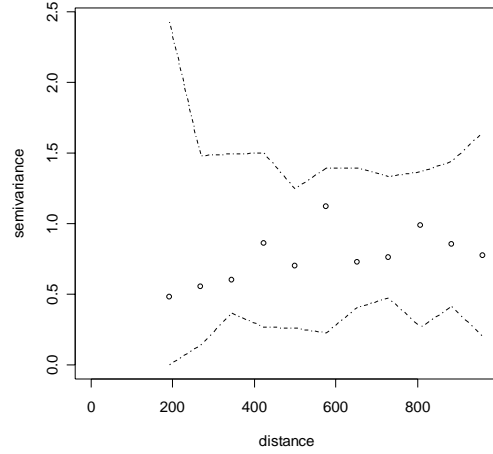
Model: $R \sim Ar + Ur$



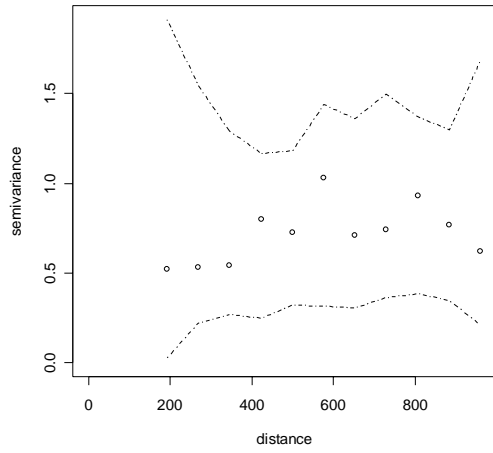
Model: $R \sim Ar + La + F + Ar*La$



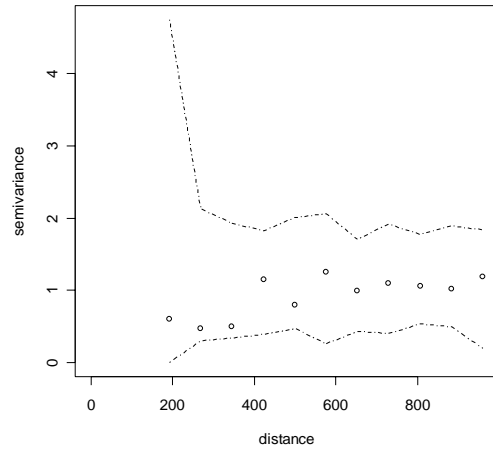
Model: $R \sim Ar + Fl$



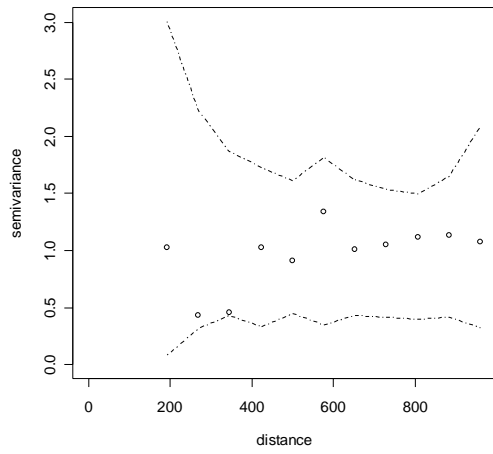
Model: $R \sim Ar$



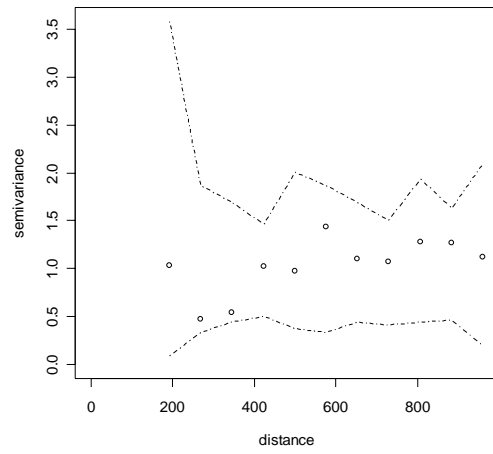
Model: $R \sim Ar + La + Ar*La$



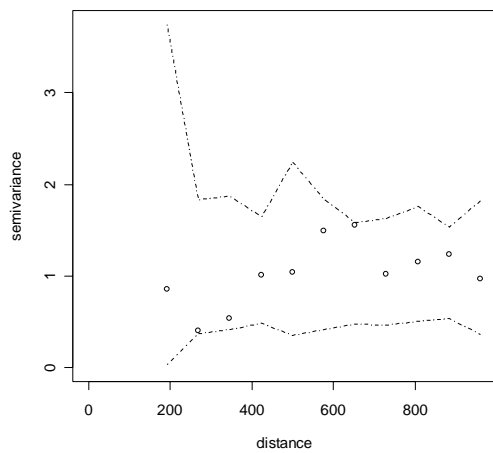
Model: $R \sim La + F$



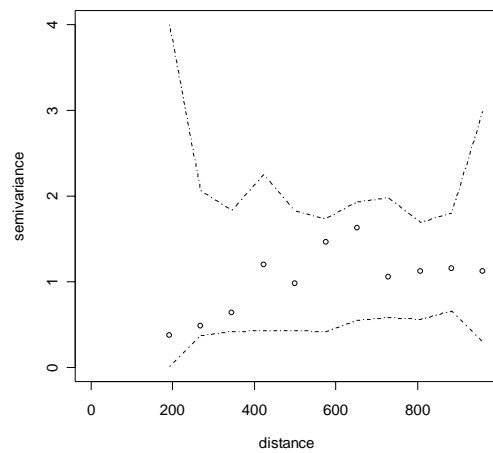
Model: $R \sim Ur + La + F + Ur*La$



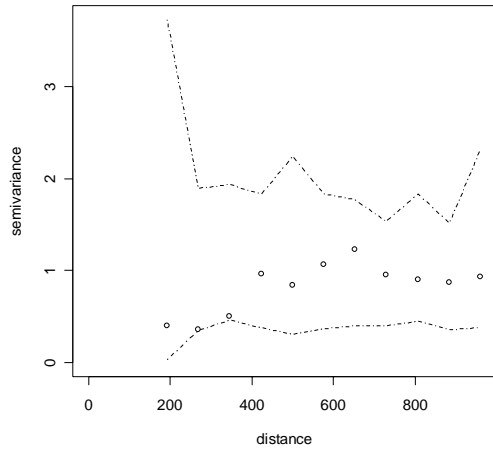
Model: $R \sim Ur$



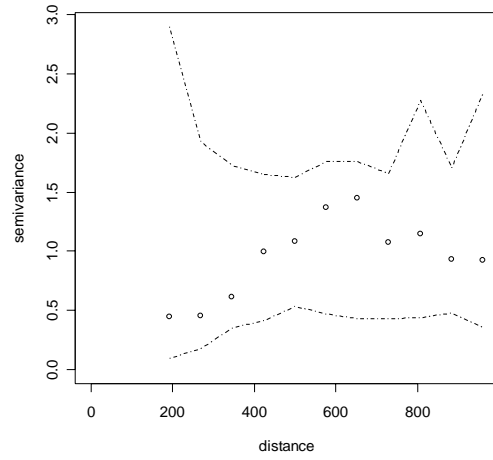
Model: $Ab \sim Ar + Ur$



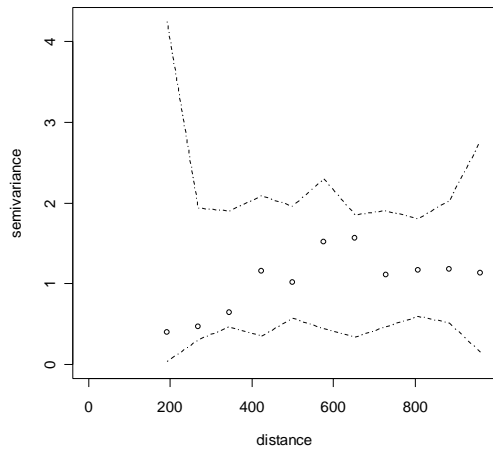
Model: $Ab \sim Ar + Fl$



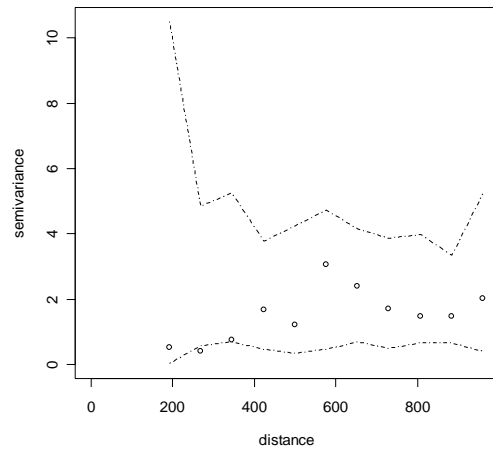
Model: $Ab \sim Ar + La + F + Ar*La$



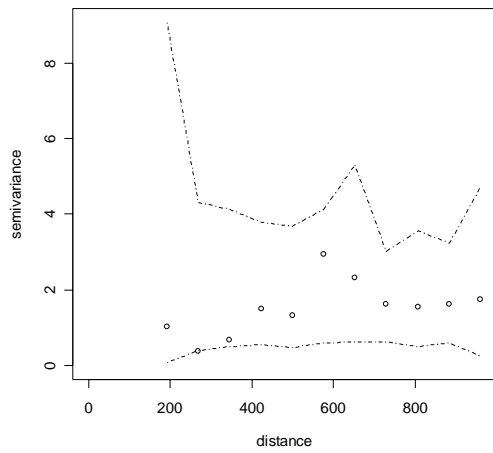
Model: $Ab \sim Ar + La + Ar*La$



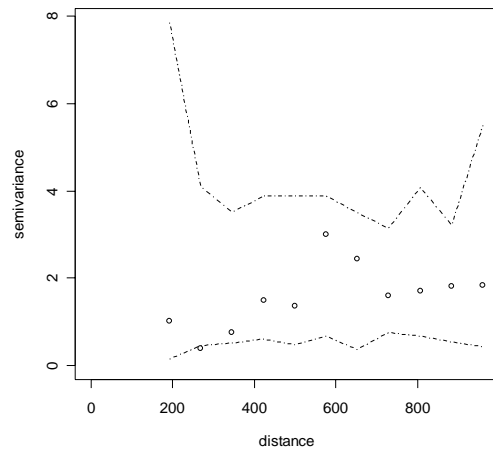
Model: $Ab \sim Ar$



Model: $Ab \sim La + F$

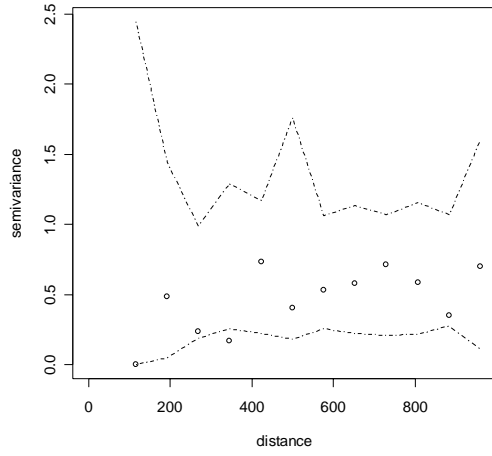


Model: $Ab \sim Ur + La + F + Ur*La$

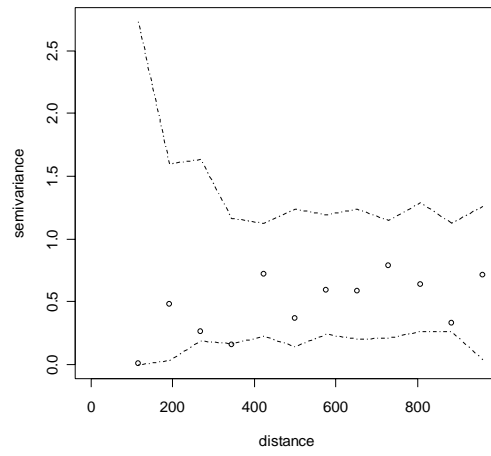


Model: $Ab \sim Ur$

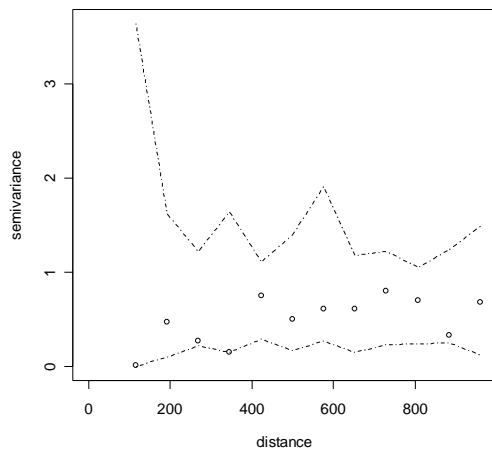
Treed habitat analysis:



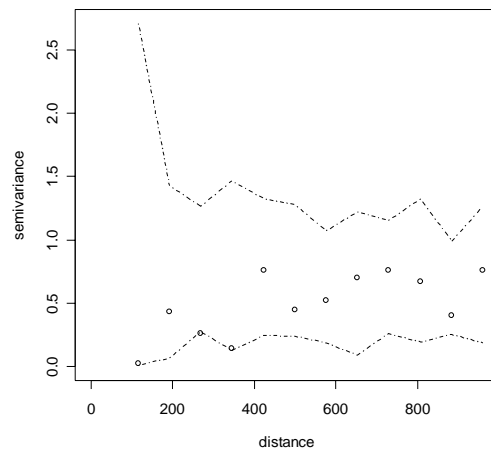
Model: $R \sim Ur + Ar$



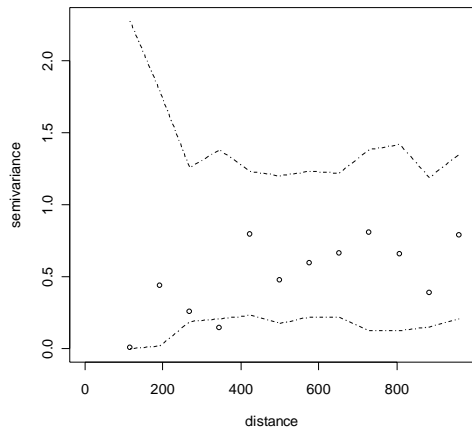
Model: $R \sim Ar + La + Ar*La$



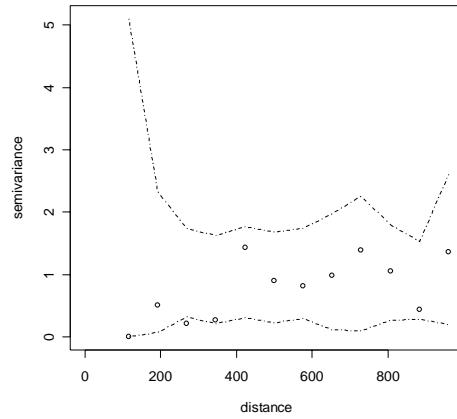
Model: $R \sim Ar + La + F + Ar*La$



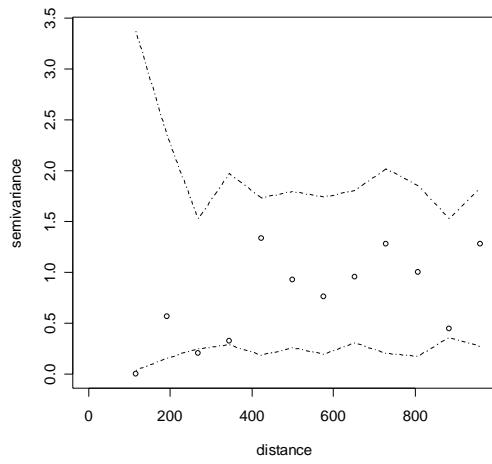
Model: $R \sim Ar + Fl$



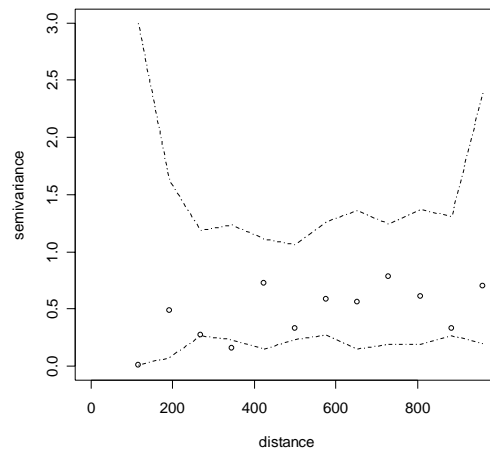
Model: $R \sim Ar$



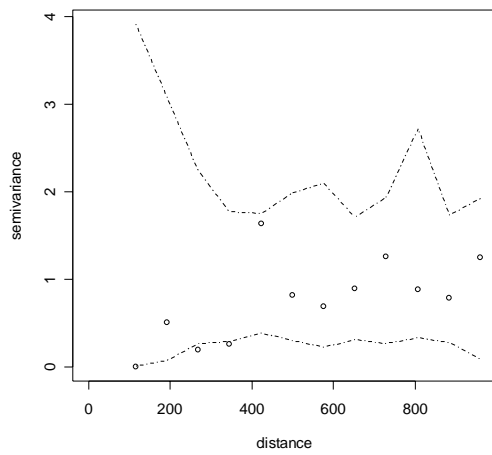
Model: $R \sim La + F$



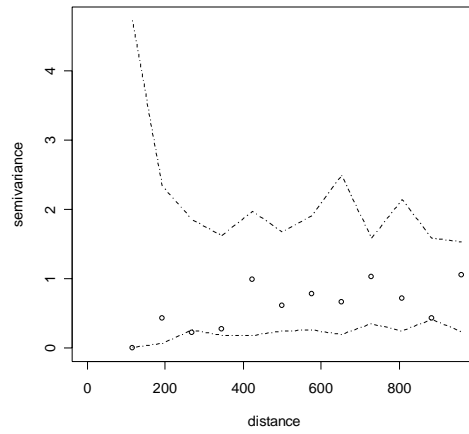
Model: $R \sim Ur + La + F + Ur*La$



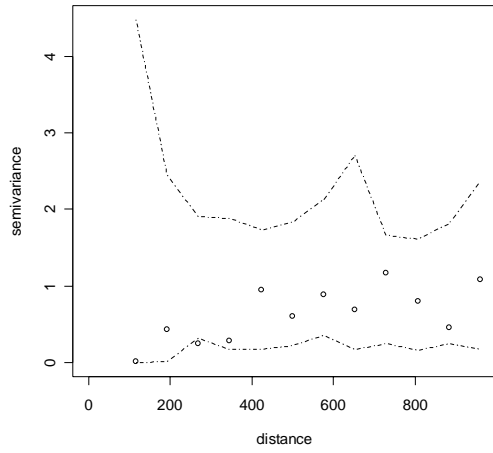
Model: $Ab \sim Ar + La + F + Ar*La$



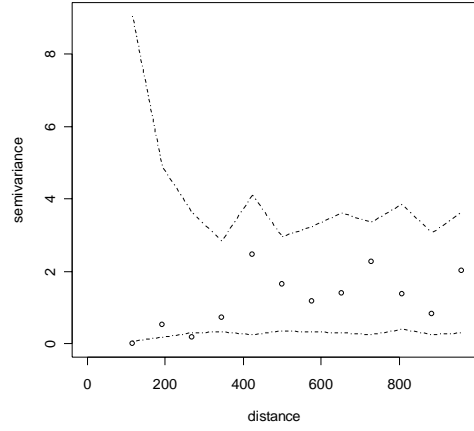
Model: $R \sim Ur$



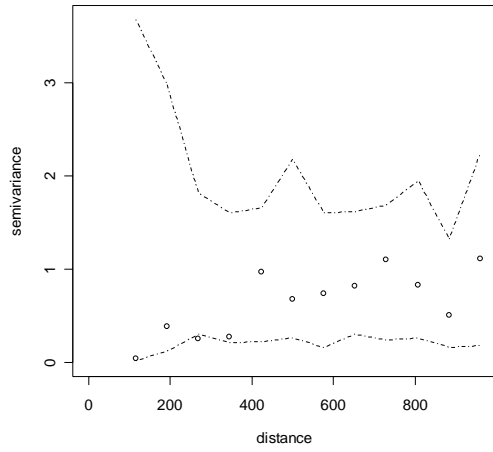
Model: $Ab \sim Ar + Ur$



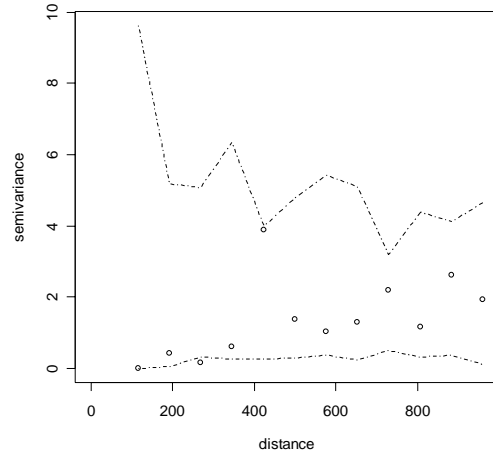
Model: $Ab \sim Ar + La + Ar*La$



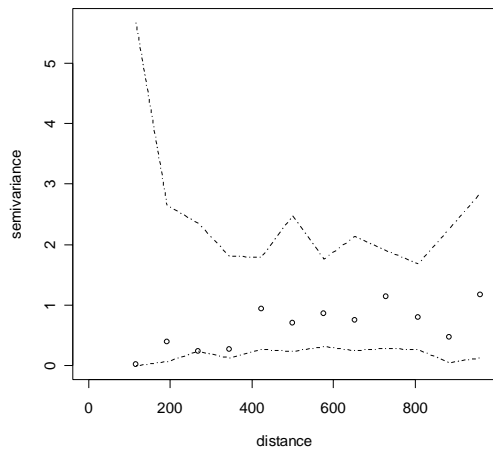
Model: $Ab \sim Ur + La + F + Ur*La$



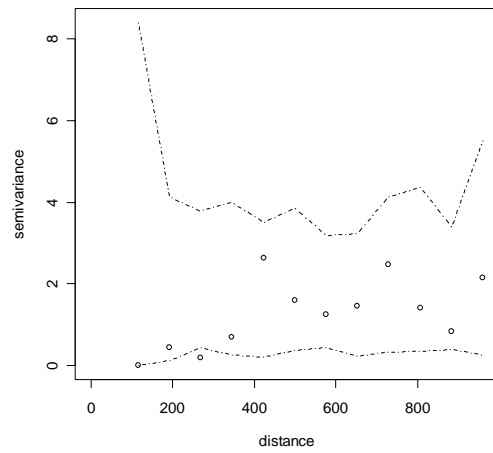
Model: $Ab \sim Ar + Fl$



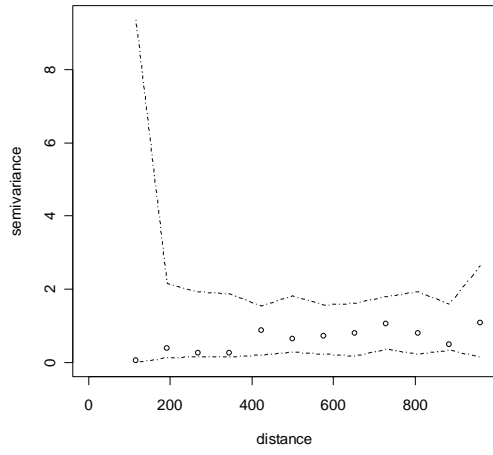
Model: $Ab \sim Ur$



Model: $Ab \sim Ar$



Model: $Ab \sim La + F$



Model: $Ab \sim Ar + V$

Appendix III: Calculations and model plots for model competitions

Forest habitat analysis – richness variable only

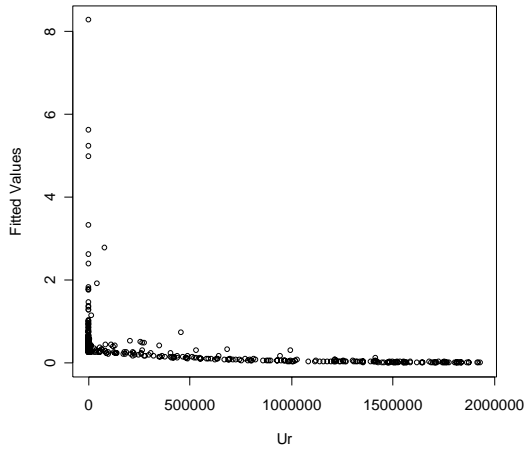


Figure III-1: plot of urban area variable and fitted values of model $R \sim Ar + Ur$.

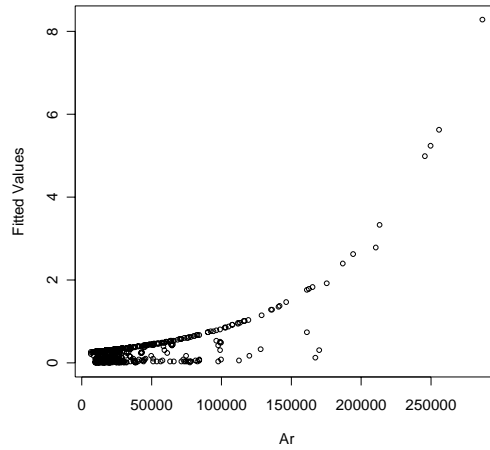


Figure III-2: plot of habitat area and fitted values of model $R \sim Ar + Ur$.

Treed habitat analysis – richness variable only

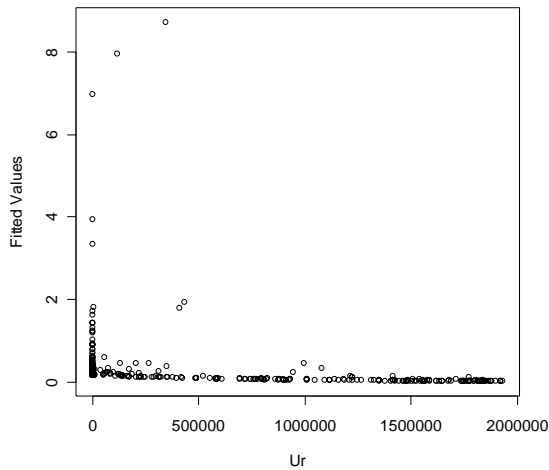


Figure III-3: plot of urbanization variable and fitted values of the model $R \sim Ar + Ur$.

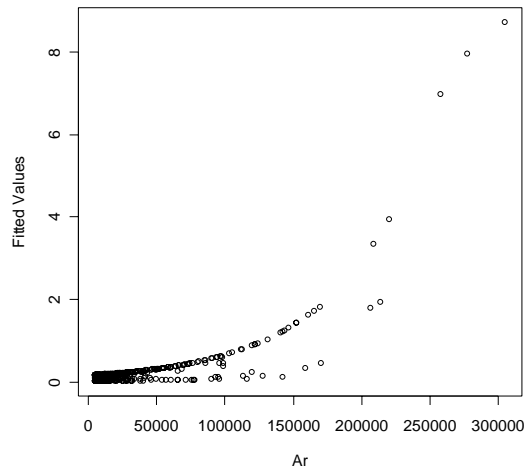


Figure III-4: plot of habitat area and fitted values of the model $R \sim Ar + Ur$.

QAIC calculations for species richness for forest habitat analysis:

Matrix showing the residual deviance and K value

$$m_1 := \begin{pmatrix} 369.81 & 4 \\ 376.21 & 6 \\ 394.36 & 5 \\ 418.71 & 4 \\ 431.44 & 3 \\ 488.52 & 6 \\ 506.44 & 3 \end{pmatrix}$$

Calculation of QAIC

$$QAIC_1 := \left(m_1^{(1)} \div 0.98046 \right) + 2 \cdot m_1^{(2)}$$

$$QAIC_1 = \begin{pmatrix} 385.180 \\ 395.708 \\ 412.219 \\ 435.055 \\ 446.038 \\ 510.256 \\ 522.533 \end{pmatrix}$$

$$n_1 := \sum \exp(-0.5 \cdot \Delta i_1)$$

$$n_1 = 1.005 \times 10^0$$

Calculation of Akaike weights.

$$\omega_{i,1} := \exp(-0.5 \cdot \Delta i_1) \div n_1$$

$$\omega_{i,1} = \begin{pmatrix} 9.948 \times 10^{-1} \\ 5.149 \times 10^{-3} \\ 1.337 \times 10^{-6} \\ 1.471 \times 10^{-11} \\ 6.061 \times 10^{-14} \\ 6.885 \times 10^{-28} \\ 1.486 \times 10^{-30} \end{pmatrix}$$

Calculation of difference between individual QAIC value and minimum QAIC.

$$\Delta i_1 := QAIC_1 - QAIC_{1,1}$$

$$\Delta i_1 = \begin{pmatrix} 0.000 \\ 10.528 \\ 27.039 \\ 49.875 \\ 60.858 \\ 125.076 \\ 137.353 \end{pmatrix}$$

$$b_1 := \sum \omega_{i,1}$$

$$b_1 = 1.000$$

QAIC calculations for species total abundance for forest habitat analysis

$$p := \begin{pmatrix} 504.11 & 6 \\ 513.65 & 4 \\ 530.49 & 5 \\ 591.4 & 4 \\ 602.68 & 3 \\ 841.7 & 6 \\ 868.14 & 3 \end{pmatrix} \quad \text{Matrix showing the residual deviance and K value}$$

Calculation of QAIC

$$QAIC_2 := \left(p^{(1)} \div 1.23127 \right) + 2 \cdot p^{(2)}$$

$$QAIC_2 = \begin{pmatrix} 421.423 \\ 425.171 \\ 440.848 \\ 488.317 \\ 495.478 \\ 695.603 \\ 711.077 \end{pmatrix}$$

Calculation of difference between individual QAIC value and minimum QAIC.

$$\Delta i_2 := QAIC_2 - QAIC_{2,1}$$

$$\Delta i_2 = \begin{pmatrix} 0.000 \\ 3.748 \\ 19.425 \\ 66.894 \\ 74.056 \\ 274.180 \\ 289.654 \end{pmatrix}$$

$$n_2 := \sum \exp(-0.5 \cdot \Delta i_2)$$

$$n_2 = 1.154 \times 10^0$$

Calculation of Akaike weights.

$$\omega_{i,2} := \exp(-0.5 \cdot \Delta i_2) \div n_2$$

$$\omega_{i,2} = \begin{pmatrix} 8.669 \times 10^{-1} \\ 1.331 \times 10^{-1} \\ 5.246 \times 10^{-5} \\ 2.583 \times 10^{-15} \\ 7.194 \times 10^{-17} \\ 2.515 \times 10^{-60} \\ 1.097 \times 10^{-63} \end{pmatrix}$$

$$b_2 := \sum \omega_{i,2}$$

$$b_2 = 1.000$$

Akaike weights sum to one.

QAIC calculations for species richness for treed habitat analysis

$$q := \begin{pmatrix} 295.65 & 4 \\ 302.7 & 4 \\ 310.29 & 5 \\ 309.67 & 6 \\ 323.79 & 3 \\ 443.66 & 6 \\ 480.30 & 3 \end{pmatrix} \quad \text{Matrix showing the residual deviance and K value}$$

Calculation of QAIC

$$QAIC_3 := \left(q^{(1)} \div 0.8516715 \right) + 2 \cdot q^{(2)} \quad \Delta i_3 := QAIC_3 - QAIC_{3,1,1}$$

$$QAIC_3 = \begin{pmatrix} 355.141 \\ 363.419 \\ 374.331 \\ 375.603 \\ 386.182 \\ 532.929 \\ 569.950 \end{pmatrix} \quad \Delta i_3 = \begin{pmatrix} 0.000 \\ 8.278 \\ 19.190 \\ 20.462 \\ 31.041 \\ 177.788 \\ 214.809 \end{pmatrix}$$

$$n_3 := \sum \exp(-0.5 \cdot \Delta i_3)$$

$$n_3 = 1.016 \times 10^0$$

Calculation of Akaike weights.

$$\omega_{i,3} := \exp(-0.5 \cdot \Delta i_3) \div n_3$$

$$b_3 := \sum \omega_{i,3}$$

$$b_3 = 1.000$$

Akaike weights sum to one.

$$\omega_{i,3} = \begin{pmatrix} 9.842 \times 10^{-1} \\ 1.569 \times 10^{-2} \\ 6.700 \times 10^{-5} \\ 3.547 \times 10^{-5} \\ 1.789 \times 10^{-7} \\ 2.438 \times 10^{-39} \\ 2.228 \times 10^{-47} \end{pmatrix}$$

QAIC calculations for species total abundance for treed habitat analysis.

$$r := \begin{pmatrix} 415.40 & 4 \\ 422.25 & 4 \\ 436.32 & 6 \\ 439.66 & 5 \\ 455.98 & 3 \\ 721.63 & 6 \\ 778.14 & 3 \end{pmatrix} \quad \text{Matrix showing the residual deviance and K value}$$

Calculation of QAIC

$$QAIC_4 := \left(r^{(1)} \div 1.049714 \right) + 2 \cdot r^{(2)} \quad \text{Calculation of difference between individual QAIC value and minimum QAIC.}$$

$$QAIC_4 = \begin{pmatrix} 403.727 \\ 410.252 \\ 427.656 \\ 428.838 \\ 440.385 \\ 699.454 \\ 747.288 \end{pmatrix} \quad \Delta i_4 := QAIC_4 - QAIC_{4,1}$$

$$\Delta i_4 = \begin{pmatrix} 0.000 \\ 6.526 \\ 23.929 \\ 25.111 \\ 36.658 \\ 295.727 \\ 343.561 \end{pmatrix}$$

Calculation of Akaike weights.

$$\omega_{i,4} := \exp(-0.5 \cdot \Delta i_4) \div n_4$$

Akaike weights sum to one.

$$\omega_{i,4} = \begin{pmatrix} 9.631 \times 10^{-1} \\ 3.687 \times 10^{-2} \\ 6.131 \times 10^{-6} \\ 3.395 \times 10^{-6} \\ 1.056 \times 10^{-8} \\ 5.853 \times 10^{-65} \\ 2.401 \times 10^{-75} \end{pmatrix} \quad b_4 := \sum \omega_{i,4} \quad n_4 = 1.038 \times 10^0$$

$$b_4 = 1.000 \quad n_4 := \sum \exp(-0.5 \cdot \Delta i_4)$$

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