EFFECTS OF FOREST LOSS AND FRAGMENTATION WITH URBANIZATION ON BIRD COMMUNITIES IN VANCOUVER

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ABSTRACT

Habitat modification with urbanization encompasses the processes of habitat loss and fragmentation. In line with the urban wildlife management goal of maximizing species diversity at the landscape and within-patch scales, it is important to understand the effects of these two processes on wildlife communities. Using Vancouver in British Columbia as the study area, I tested the hypotheses that (1) loss in forest area in the landscape with urbanization results in bird extirpations as expressed by the species-area function; and (2) fragmentation of the remaining forest into fragments with urbanization results in large fragments having greater bird species richness and densities than small fragments because large fragments contain a greater diversity and/or abundance of habitat resources. Prior to European settlement in 1859, Vancouver was covered completely by coastal western hemlock forest. By estimating the area of forest loss in Vancouver since 1859 and reviewing the conservation status of birds in Vancouver, I show that the observed number of bird extirpations due to forest loss matches that predicted by the species–area function for bird species closely associated with lowland coastal temperate forests and restricted in their geographic distribution in British Columbia. Using bird and habitat data collected in 14 forest fragments in Vancouver and lower West Vancouver, I show that large fragments support higher bird species richness and density than small fragments in spring, summer and fall. This could be attributed to large fragments containing a greater diversity and/or abundance of habitat resources, especially tree species diversity and abundance of decaying standing material. However, this mechanism is unable to satisfactorily explain all the patterns across seasons. I also found that bird species richness and density were responding to habitat resources that remained constant with area. Hence, there is a possibility that birds may not even select for large fragments despite the greater diversity and/or abundance of habitat resources, if resources that are independent of area are changed dramatically.

TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

CHAPTER 1

INTRODUCTION

The United Nations Population Division has estimated that the world population is currently 6.1 billion and will increase to 8.1 billion by 2030 (UNPD 2001). Much of the world population is also increasingly concentrated in urban[1] areas. In North America, the proportion of the population in urban areas was 64% in 1950, compared to 77% in 2000. The proportion of the population in urban areas in North America is likely to increase to 84% by 2030 (UNPD 2000).

A consequence of urban population growth is the expansion of urban areas, which is typically accompanied by extensive habitat modification in and around these areas (Sharpe et al. 1986). The modification of habitat with urbanization constitutes two processes: habitat loss as habitat is converted to impervious man-made structures (i.e. buildings, residential houses, roads etc), and habitat fragmentation as the remaining habitat is sub-divided into isolated fragments of varying sizes by these man-made structures (Marzluff and Ewing 2001). The loss in habitat with urbanization has a greater degree of permanence, unlike that encountered with forestry and agriculture. With forestry and agriculture, native vegetation is allowed to regenerate or is replaced by crops (Marzluff and Ewing 2001). The landscape matrix following urbanization is also less permeable to wildlife (McIntyre and Hobbs 1999).

Habitat loss and fragmentation have been linked to a decline in native wildlife. This decline is possibly due to changes in habitat resources and microclimate, and the disruption of dispersal routes (Wilcove et al. 1986; Saunders et al. 1991; Andren 1994). Secondary effects,

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[1] The terms "urban", "suburban" and "rural" refer to different stages along the urbanization continuum. The rural end has the least human population density and is the most "natural", while the urban end has the highest population density (usually defined as greater than 620 persons/km^2) and the least amount of natural landscape elements. The suburban zone is usually defined as the intermediate stage between the urban and rural (McDonnell and Pickett 1990). Often the urban and suburban zones are not well delineated. Throughout this thesis, the term "urban" is used loosely to encompass both the urban and suburban zones within this continuum.

such as increased exposure to mesopredators and exotic species, can further contribute to the decline in native wildlife (Crooks and Soulé 1999; Kerpez and Smith 1990). Researchers also recognize that the effects of habitat loss can be much greater than the effects of habitat fragmentation, at least with bird populations (Fahrig 1997; Trzcinski et al. 1999). Hence, both processes should be dealt with independently.

The goal of urban wildlife management is often the maximization of species diversity at the landscape and within-patch scales (i.e. gamma and alpha diversities, Whittaker 1972), rather than the preservation of every remaining species (Murphy 1988; Raedeke and Raedeke 1995). This requires an understanding of the effects of habitat loss and fragmentation with urbanization on wildlife communities. Our understanding of the effects of these processes have come mainly from studies conducted in landscapes modified by agriculture or forestry (Figure 1). Conservation strategies based on studies in forested and agricultural landscapes may not be applicable to urban landscapes due to differences in the permanence of habitat loss and permeability of the matrix to wildlife. Consequently, more research in urban landscapes is required.

To understand the effects of habitat loss and fragmentation with urbanization on wildlife communities, urban ecologists have been interested in two questions (Juricic and Jokimaki 2001): (1) Does habitat loss with urbanization result in the extirpation of native wildlife? (2) Do large habitat fragments contain more wildlife species and greater densities than small fragments in existing urban landscapes? Here, I address these questions by reviewing the literature pertaining to birds. References to bird communities in agricultural-urban landscapes are used to supplement those from wholly urban landscapes, where appropriate. I further discuss the evidence in the context of the area *per se* and habitat diversity hypotheses. Finally, I establish the hypotheses and predictions that form the basis of this study. The focus here is on birds because they have been the main subjects of most wildlife studies in urban landscapes (Marzluff et al.

1998; Savard et al. 2000). I also focussed only on the community-level indicators of species richness and density because urban wildlife managers and planners often rely heavily on community-level information to make management decisions, within a narrow time window. However, I acknowledge the importance of considering demographic responses, including fecundity, survivorship, immigration and emigration, in order to justify long-term decisions.
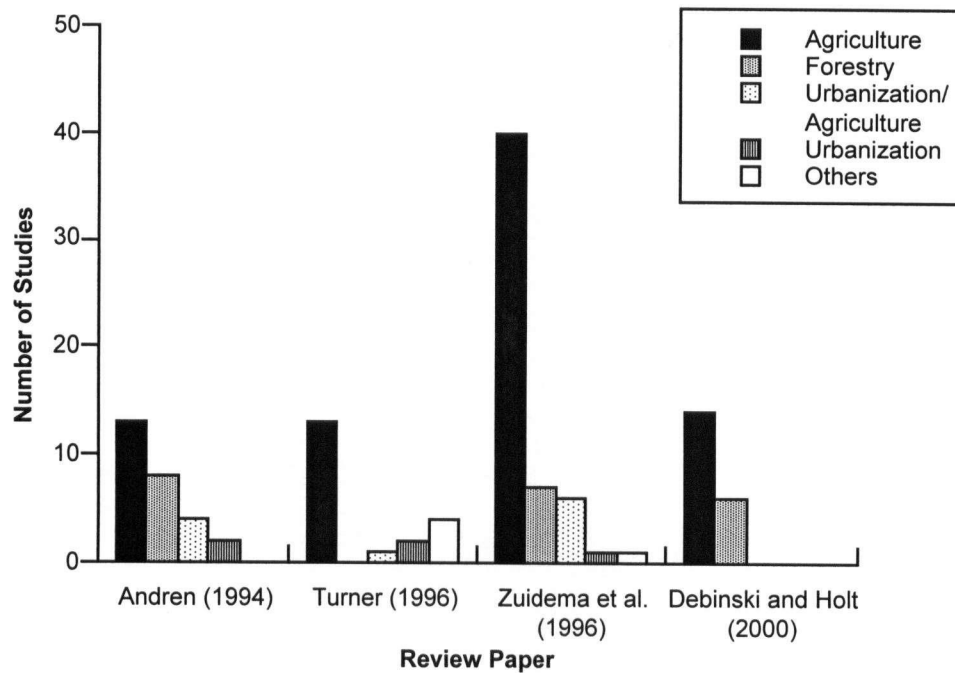
Figure 1. Number of studies, in terms of the agents of habitat modification, cited in four review papers pertaining to habitat fragmentation and wildlife communities.

This survey showed that a disproportionate number of studies came from landscapes modified by agriculture. Studies from wholly urban landscapes are few. "Agriculture" included cropping, pastoralism and ranching. "Forestry" included native forest and plantation operations. "Urbanization/Agriculture" referred to the dominance of urbanization and agriculture in the landscape. "Urbanization" referred to the replacement of habitats with urban development. "Others" included commercial cash-crop farming such as coffee, tea and fruit.

LITERATURE REVIEW

Does habitat loss with urbanization result in the extirpation of native bird species?

Research on the effects of habitat loss with urbanization often involves the comparison of the pre- and post-development bird species composition at a given site. Aldrich and Coffin

3

(1980) first surveyed a 38-hectare mature deciduous forest at Lake Barcroft, Washington D.C., in 1942. They re-surveyed the entire area in 1979, after most of the forest was cleared for urban development. Their results revealed the extirpation of three breeding forest bird species, Red-eyed Vireo (*Vireo olivaceus*), Ovenbird (*Seirus aurocapillus*) and Scarlet Tanager (*Piranga olivacea*). Similar extirpation of native bird species due to habitat loss with urbanization has been reported by Batten (1974), Walcott (1974) and Kattan et al. (1994).

Further comparisons of bird communities between two or more sites of differing degree of urban development also support the notion that some groups of bird species tend to be more affected by habitat loss with urbanization than others. Lancaster and Rees (1979) compared bird communities of several industrial and suburban residential sites, and a mixed conifer-deciduous forest fragment in Vancouver, British Columbia. They found that urban habitats were dominated mainly by omnivores and granivores, including the House Sparrow (*Passer domesticus*) and European Starling (*Sturnus vulgaris*). In contrast, the bird community in the mixed conifer-deciduous forest fragment comprised mainly of insectivores, some of which are dependent on forest (e.g. Varied Thrush *Ixoreus naevius* and Golden-crowned Kinglet *Regulus satrapa*). Beissinger and Osborne (1982) also demonstrated a shift in the bird community from one that was dominated by canopy foliage and bark-gleaning insectivores to one that was dominated by ground-gleaning insectivores, with the conversion of beech-maple forest to residential area in Oxford, Ohio. Similar conclusions were reported in other studies (Emlen 1974; Gavareski 1976; DeGraaf and Wentworth 1981, 1986; Blair 1996; Sewell and Caterrall 1998). The importance of habitat fragments in maintaining bird species richness in urban landscapes is further corroborated by observations of increases in the abundance of native bird species in urban areas in close proximity to existing habitat fragments (Munyenyembe et al. 1989; Germaine et al. 1998; Melles et al. 2002). These studies highlight that habitat loss with urbanization will result potentially in the extirpation of native bird species.

4

The hypothesis that bird extirpations will occur as a single large and contiguous habitat is reduced in area by urbanization or any other human actions is based upon the hypothesis that area alone is important. This area *per se* hypothesis stems from the equilibrium theory of island biogeography (MacArthur and Wilson 1967). The theory states that the number of species on an island is a dynamic equilibrium maintained by the rates of immigration from a larger species pool and extinction on the island. The rate of extinction is expected to increase as island area decreases because population sizes become smaller and more sensitive to demographic stochasticity. The power form of the species–area function ($S = cA^z$, where S is the number of species and A is habitat area, c and z are constants) was derived from this theory.

In recent years, the species–area function has been used to predict species extirpations from the area of habitat loss. A match between the observed number of extirpations and that predicted by the function is also often taken as evidence of the area *per se* hypothesis (Simberloff 1988). Pimm and Askins (1995) used the species–area function to predict the number of bird extirpations that would have resulted from the clearing of forests in eastern North America. They found that the observed number of extirpations was comparable to that predicted by the species–area function. Similar results were reported by other studies in tropical forests (Brooks et al. 1997; Brooks et al. 1999; Castellata et al. 2000). Hence, there appears to be some support for the area *per se* hypothesis. However, this has not been adequately replicated across forest types and landscapes. The only study conducted in urban landscapes is that by Castellata et al. (2000) in tropical Singapore. There has been no similar study in temperate regions.

There are three caveats on the use of the species–area function to predict species extirpations from the area of habitat loss and hence test the area *per se* hypothesis. Firstly, the use of this approach should include only species that are closely associated with the habitat of concern and are either endemic or restricted in their geographic distribution. The argument is that a species is most likely to become extirpated with the loss of a particular habitat if it is

5

highly dependent on that habitat for part or all of its life history requirements (Pimm and Askins 1995). Also, a species restricted in its geographic distribution is less likely to be rescued by individuals from other nearby populations and is more susceptible to extirpation from a loss in habitat (Brown 1984; Lawton 1993; Brooks et al. 1997). Secondly, there is a time-lag between habitat loss and eventual extirpation of species. Extirpation of species following habitat loss typically occurs over prolonged relaxation times (Diamond 1972; Tilman et al. 1994). Hence, comparison of the observed and predicted number of extirpations should not just include species that have been extirpated, but also those that are currently declining and likely to be extirpated with time (Brooks et al. 1999). Thirdly, use of the species–area function to predict extirpations is dependent on the value of the constant z. Generally, the z-value is between 0.12–0.18 for nested areas within continuous forests; it approaches 0.25, with a range of 0.25–0.35, for "archipelagoes" of forest fragments and lies between 0.6–1 for highly isolated forest fragments (Rosenzweig 1995). Often, the z-value of 0.25 is used because most landscapes resemble an "archipelago" of forest fragments (Pimm and Askins 1995; Brooks et al. 1997; Brooks et al. 1999; Castellata et al. 2000).

There is sufficient evidence in the literature to suggest the extirpation of native bird species as a result of habitat loss with urbanization. Such extirpations in urban landscapes present an opportunity to test the area *per se* hypothesis by comparing the observed number of extirpations to that predicted by the species–area function.

Do large habitat fragments contain more bird species and greater densities than small fragments in existing urban landscapes?

Bird species richness–fragment area relationships

With urbanization, the remaining habitat within the landscape is also fragmented or sub-divided into isolated fragments of varying sizes. Several studies of habitat fragments in urban

landscapes in North America and elsewhere in the world have reported that large fragments will support more bird species than small fragments (Gotfryd and Hansell 1986; Tilghman 1987a; Soulé et al. 1988; Grover and Slater 1994; Natuhara and Imai 1999; Park and Lee 2000). Studies of habitat fragments in agricultural-urban landscapes in eastern United States further revealed that increases in bird species richness with fragment area could be attributed to the increased number of area-sensitive species in large fragments. Working in forest fragments of Maryland, Whitcomb et al. (1981) and Lynch and Whigham (1984) reported that the number of forest-interior species was correlated positively with fragment area, whereas the number of edge species was correlated negatively to fragment area. In another study within the same region, Robbins et al. (1989) reported that 19 of 26 bird species that were likely to occur only in large fragments were neotropical migrants.

Most of the evidence of large fragments supporting greater bird species richness has come from studies conducted in the breeding season. Although there has been some work on wintering bird communities in the urban landscape, they have been conducted mainly in man-made urban habitats (DeGraaf 1991; Jokimaki et al. 1996; Jokimaki and Suhonen 1998). In one of the few studies of wintering bird communities in habitat fragments within the urban landscape, Tilghman (1987b) showed that large woodland fragments surrounded by urban development supported more bird species than small fragments in winter in Springfield, Massachusetts. This relationship was less pronounced than that observed in the breeding season (Tilghman 1987a). Studies in agricultural landscapes seemed to show the opposite: species–area relationships were non-existent during winter (Yahner 1985; Hamel et al. 1993; McIntyre 1995).

Published data relating bird species richness to habitat fragment area must however be interpreted cautiously. Generally, attempts to show that large fragments support more bird species than small fragments involve sampling efforts that are proportional to fragment area. The aim is to ensure equivalent effort per unit area. While this is necessary to ensure that all bird

7

species within the fragments are enumerated, it introduces a bias from sampling effort alone (Connor and McCoy 1979; McGuinness 1984; Woolhouse 1987). Increased sampling effort results in the detection of more species in large fragments. Hence, the observed positive relationship between bird species richness and fragment area could be an artefact of sampling.

Various statistical methods can be used to eliminate the possibility that increases in species richness with fragment area is the result of greater sampling effort. The most commonly used method is rarefaction. Rarefaction reduces each sample to a standard of constant size. It calculates the number of species expected in each fragment, corresponding to a standard size or number of individual birds in all fragments (e.g. 10 individuals). The latter is often the number of individuals in the sample with the fewest individuals (Magurran 1988). Hart and Horwitz (1991) used rarefaction to illustrate the potential dangers of not testing for the effects of variable sampling effort when interpreting observed bird species richness and fragment area patterns. They used the data of Bostrom and Nilsson (1983), who showed that bird species richness in raised peat bogs in Sweden was positively correlated to bog area. The bogs had been surveyed by transects of lengths that were proportional to bog area. Hart and Horwitz rarefied the number of bird species detected in each bog and re-fitted the expected number of bird species in each bog to area. They did not observe a relationship between bird species richness and area upon rarefaction, and concluded that the initial species–area pattern was an artefact of sampling.

The observation that large habitat fragments will support more bird species than small fragments in urban landscapes or any other fragmented landscape has commonly been associated with two hypotheses. The first relates to the area *per se* hypothesis (i.e. large fragments have lower rates of extinctions and hence support a higher number of species than small fragments). The test of this hypothesis with fragments of varying sizes is often based on a fit of species richness data from these fragments to the species–area power function. This is commonly applied in studies of bird species richness in habitat fragments within urban landscapes (e.g.

Gotfryd and Hansell 1986; Tilghman 1987a, b; Soulé et al. 1988; Grover and Slater 1994; Park and Lee 2000). There are two problems with this approach. Firstly, it provides a single snapshot of patch occupancy from which local extinctions in small fragments are inferred by comparison to the species composition in large fragments. This can be misleading because not all bird species were necessarily present initially in each fragment (Bolger et al. 1991). A rigorous test of this hypothesis would entail the documentation of species extirpations in each fragment at multiple time points (Crooks et al. 2001). Such studies are logistically difficult because they require the long-term monitoring of bird communities within a group of habitat fragments. The second problem is that it is difficult to separate the effect of area *per se* from that of habitat differences between the fragments. Attempts to control for habitat differences by selecting only fragments that are relatively similar in vegetation characteristics are usually futile (e.g. Gotfryd and Hansell 1986; Soulé et al. 1988; Robbins et al. 1989).

The second hypothesis relates to the notion that large fragments can support a higher number of species than small fragments because they contain a greater diversity and/or abundance of habitat resources (Williams 1964; Lack 1969). This habitat diversity hypothesis is founded on the premise that habitat quality is an important determinant of species richness. For birds, the diversity and/or abundance of habitat resources, as measured by structural and floristic descriptors, are good predictors of species richness (e.g. MacArthur and MacArthur 1961; Willson 1974; Roth 1976; James and Warmer 1982; Erdelen 1984).

Acceptance of the habitat diversity hypothesis requires the validation of three predictions: (1) species richness will respond positively to area; (2) habitat variables describing the diversity and/or abundance of habitat resources will vary positively with area; (3) species richness will also respond positively to the habitat variables that vary positively with area (Figure 2). Using this protocol, some authors have demonstrated that positive bird species–area relationships on oceanic islands and naturally occurring habitat islands could be attributed to a greater diversity

9

of habitat resources (Power 1972, 1976; Johnson 1975; Martin et al. 1995). Urban and Smith (1989) used a forest-simulation model and a known data set of tree size classes from a 9-ha forest to generate a scenario of habitat changes over 750 years. They then used bird–habitat models to predict species richness corresponding to these habitat changes. Comparing bird species richness in quadrats of 1 to 9 ha, they showed that larger quadrats had greater bird species richness, which was in turn the result of a greater diversity of habitat resources as approximated by the greater variation in tree classes. However, Freemark and Merriam (1986) did not find evidence to support this hypothesis in forest fragments on farmland in Ontario. They found that bird species richness increased with habitat heterogeneity, but not with fragment area.

Species Richness | Habitat Resource (diversity/ abundance) | Species Richness | Habitat Resource (diversity/abundance)

Area | Area

Prediction (1) | **Prediction (2)** | **Prediction (3)**
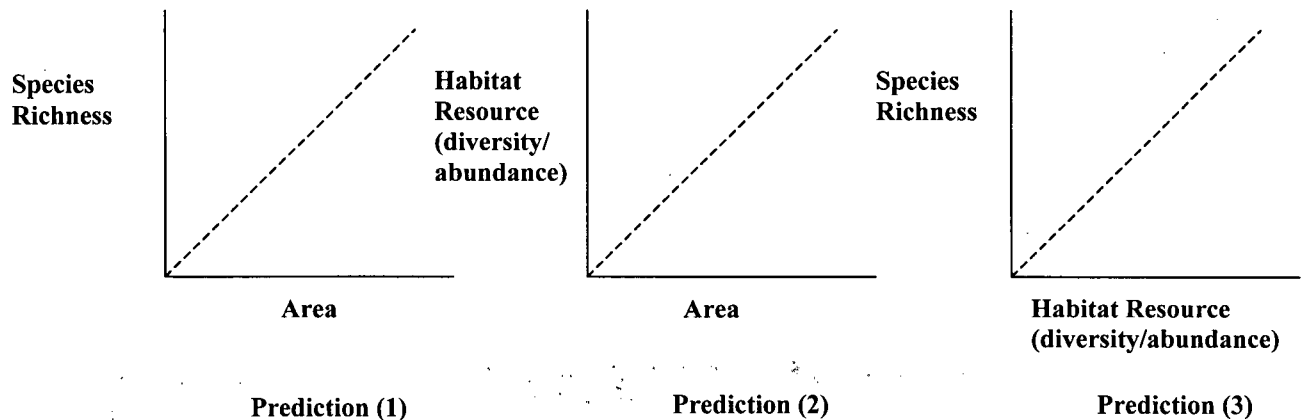
Figure 2.   Theoretical predictions deriving from the habitat diversity hypothesis.

The predictions as depicted follow that described in the text. The habitat resource variable in Prediction (2) is the same variable as that in Prediction (3). The relationships need not be linear.

The empirical evidence that would support this hypothesis in relation to habitat fragments in both urban and agricultural-urban landscapes is mixed. Working in forest fragments surrounded by an agricultural-urban landscape matrix in Maryland, Lynch and Whigham (1984) reported that an observed positive bird species–area relationship was likely the result of the positive correlation between fragment area and canopy cover. Grover and Slater (1994) also demonstrated that large *Melaleuca* forest fragments contained greater bird species richness than

10

small fragments because of greater understorey vegetation density in suburban Brisbane, Australia. In contrast, Ambuel and Temple (1983) did not find any area-dependent trends in vegetation structure or composition in woodlots within an agricultural-urban landscape in Wisconsin. Working in a similar landscape type around New London, Connecticut, Askins et al. (1987) also dismissed the notion that observed increases in bird species richness with forest fragment area was related to area-dependent changes in habitat variables. Interestingly, they reported a correlation coefficient of 0.45 between fragment area and tree species diversity (significant at $\alpha=0.05$, $r_{0.05, 44} = 0.291$, Zar 1984). Tree species diversity was also reported in their study to be important in predicting the number of forest-interior bird species in the fragments. It appears that the habitat diversity hypothesis may in some cases account for increases in bird species richness with fragment area.

Two assumptions are associated with these empirical tests of the habitat diversity hypothesis. Firstly, it is assumed that birds will respond only to habitat resources that vary with area. This may not be so as shown by some studies (e.g. Ambuel and Temple 1983; Lynch and Whigman 1984; Askins et al. 1987; Robbins et al. 1989). Habitat resources that are independent of area may be just as important. Secondly, it is assumed that bird responses to habitat resources are similar across seasons. This is not the case. Fretwell (1972) predicted that the habitat breadth of birds (as defined by the number of habitat resource types used by birds) should become narrower in winter than summer, due to reduced availability of resources in winter. This coupled with habitat requirements for nesting means that birds will respond to more and different habitat variables in summer than in winter (Rice et al. 1980; Rice et al. 1983; Anderson et al. 1983; Morrison et al. 1985; Manuwal and Huff 1987; Wiebe and Martin 1998).

Bird density–fragment area relationships

As with bird species richness, positive correlations between bird density (number of individuals per unit area) and fragment area have been reported in both urban (e.g. Tilghman 1987a) and agricultural-urban landscapes (e.g. Lynch and Whigman 1984; Askins et al. 1987). However, interpretation of the bird density–area relationship has received less attention than the bird species–area relationship. Only recently, have there been attempts to link the density–area relationship to either the area *per se* or habitat diversity hypothesis. If the habitat diversity hypothesis is correct, bird density would respond positively to area and to habitat variables that vary positively with area, similar to responses observed for bird species richness. There are two reasons for this. Firstly, population density is intrinsically linked to species richness in that species with low densities are more likely to have less viable populations (Diamond 1984; Gilpin and Soulé 1986; Crooks et al. 2001). Secondly, the theory of island biogeography assumes that the number of individuals increases linearly with area and hence density is assumed to be constant for all areas (MacArthur and Wilson 1967: 13). As the area *per se* hypothesis is derived from island biogeography theory, this phenomenon of density compensation is expected. Hence, if density is not constant with area, then it suggests that some other factors such as the diversity and/or abundance of habitat resources may be more important. Meta-analysis of published data pertaining to bird density–area relationships suggested that densities tended to show moderate to large positive correlations with area (Bender et al. 1998; Connor et al. 2000). Connor et al. (2000) further argued, on the basis of this observed trend of positive density–area correlation, that habitat resources (and hence the habitat diversity hypothesis) and not area *per se* appeared to be the dominant factor driving bird–area–habitat relationships. Similar arguments based on empirical field data have also been presented by other authors (e.g. Diamond 1970; Haila and Jarvinen 1983; Martin et al. 1995).

In this review, I point out that the habitat diversity hypothesis suggests the possibility of another mechanism other than area *per se* that may be driving observed patterns of increased bird species richness and densities with fragment area. However, evidence of the habitat diversity hypothesis does not necessarily eliminate the area *per se* hypothesis. Nevertheless, the habitat diversity hypothesis can provide useful directions for restoration efforts aimed at enhancing habitat quality and maximizing within-patch species diversity. It is also apparent from this review that investigations of bird–area–habitat relationships in wholly urban landscapes are lacking. Even more striking is that most of the work on habitat fragments in urban landscapes in North America comes from the east. There have been few studies in the Pacific Northwest, a concern echoed by Ferguson et al. (2001).

HYPOTHESES AND PREDICTIONS

In this study, I investigated the effects of forest loss and fragmentation with urbanization on bird communities in Vancouver, British Columbia. By "forest loss and fragmentation with urbanization", I am referring specifically to the conversion of forest to urban development, and the sub-division of the remaining forest into isolated fragments of varying sizes by urban development. I examined two hypotheses:

(1) Loss in forest area in the landscape with urbanization results in bird extirpations as expressed by the species–area function (i.e. area *per se* hypothesis).

(2) Fragmentation of the remaining forest with urbanization results in large fragments having greater bird species richness and densities than small fragments because large fragments contain a greater diversity and/or abundance of habitat resources (i.e. habitat diversity hypothesis).

To validate these hypotheses, I tested the respective predictions that would be expected if the hypotheses are correct.

Prediction pertaining to Hypothesis (1):

(a) Observed number of bird extirpations due to the loss in forest area matches that predicted by the species–area function.

Predictions pertaining to Hypothesis (2):

(a) Bird species richness in forest fragments responds positively to fragment area, and to the diversity and/or abundance of habitat resources that vary positively with area, after correcting for the effects of sampling effort.

(b) Bird species richness in forest fragments does not respond to the diversity and/or abundance of habitat resources that remain constant with fragment area, after correcting for the effects of sampling effort.

(c) Overall bird density and density of functional bird groups in forest fragments respond positively to fragment area, and to the diversity and/or abundance of habitat resources that vary positively with area.

(d) Overall bird density and density of functional bird groups in forest fragments do not respond to the diversity and/or abundance of habitat resources that remain constant with area.

These predictions were tested across four seasons, "Spring", "Summer", "Fall" and "Winter".

In Chapter 2, I describe the study area and the methods used to test the hypotheses and predictions. The results are summarized in Chapter 3. These are structured according to the order in which the hypotheses and predictions are outlined above. In Chapter 4, I discuss the results in the context of the hypotheses and explore the implications on land-use planning and management of habitat fragments in urban landscapes. Finally, in Chapter 5, I reiterate the key findings of this study.

CHAPTER 2

METHODOLOGY

STUDY AREA

The study area comprised the Vancouver municipality and University Endowment Lands (collectively referred to in this thesis as "Vancouver"), and the lower part of the West Vancouver municipality in British Columbia, Canada (49° N, 123° W) (Figure 3). The study area is within the Fraser lowland, and the Georgia Depression ecoprovince (Demarchi et al. 1990). The study area experiences warm and dry summers, and cool and wet winters. Temperatures average 18°C in summer and 3°C in winter, while annual precipitation ranges from 1100–1600 mm. Slightly higher than normal mean daily temperature was recorded in November, while higher than normal total monthly precipitation was recorded for April, August and December during the study (April to December 2001) (Meteorological Service of Canada 2002) (Appendix I).

The vegetation of the study area is representative of the Coastal Western Hemlock biogeoclimatic zone (Pojar et al. 1991). It was covered by coastal western hemlock forest in the past (Slaymaker et al. 1992; Macdonald 1992). The forest canopy was dominated by coniferous species, including western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*). Douglas-fir (*Pseudotsuga menziesii*) occurred only on drier sites. Deciduous broadleaved trees, such as red alder (*Alnus rubra*), bigleaf maple (*Acer macrophyllum*) and bitter cherry (*Prunus emarginata*), dominated the coast and waterways, and areas subjected to natural disturbance (e.g. fire, wind-throw). The understorey was comprised of a shrub layer dominated by salal (*Gaultheria shallon*), red huckleberry (*Vaccinium parvifolium*) and red elderberry (*Sambucus racemosa*) on undisturbed sites, and salmonberry (*Rubus spectabilis*), thimbleberry (*Rubus*

parviflorus) and vine maple (*Acer circinatum*) on disturbed sites (Pojar et al. 1991; Slaymaker et al. 1992).
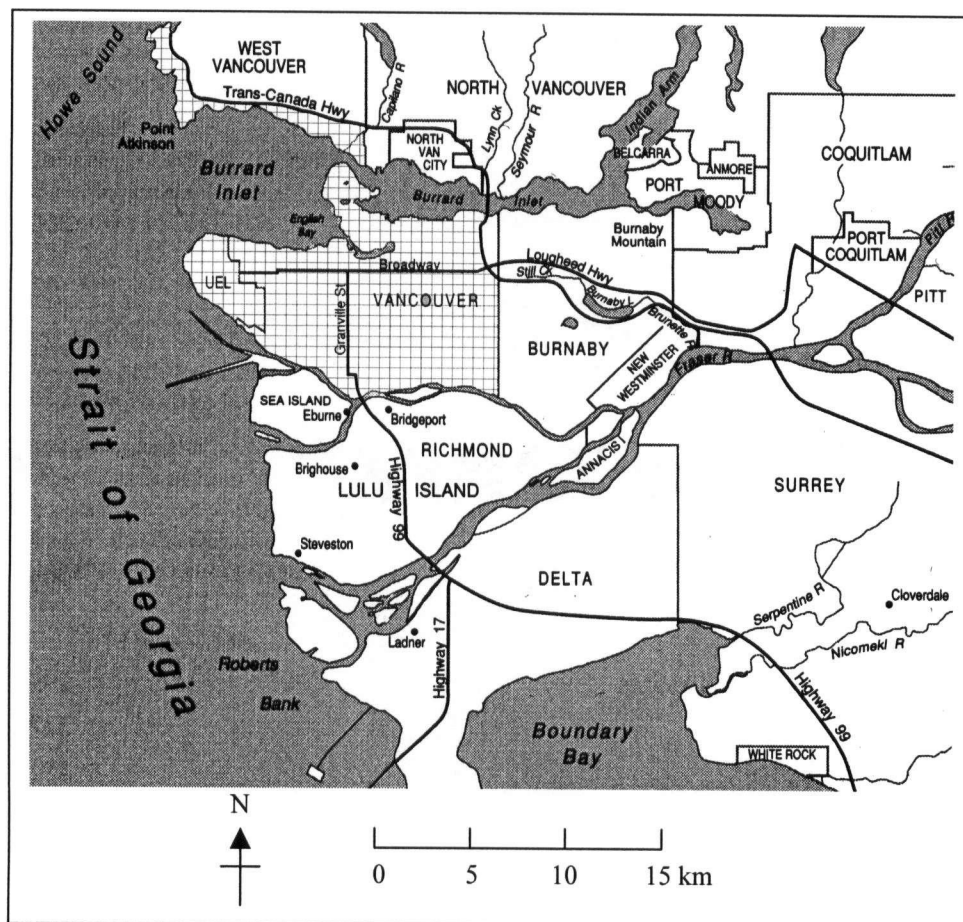
Figure 3.   Location of study area (hatched), which comprised of the municipality of Vancouver and the University Endowment Lands (UEL) (referred to in the rest of this thesis as "Vancouver") and the lower part of the municipality of West Vancouver.

Logging of the forests in the study area commenced in early 1860, when the British advanced westwards from New Westminster in search of lumber. By 1900, most of these forests were logged and burnt (Harris 1992; Macdonald 1992). The drier soil resulting from the fires favoured the regeneration of Douglas-fir over western hemlock or western redcedar. The extensive disturbance due to logging also resulted in the regeneration of a dense rank of red alder and bigleaf maple in the canopy and an equally dense shrub layer dominated by salmonberry (Oke et al. 1992). This disturbance brought about a second-growth mixed conifer-deciduous forest, which is evident in the present landscape (GVRD 1992). Much of these second-growth

16

forests were replaced and fragmented by urban development over a span of 30 years, from 1900–

1929[2]. A second, but less protracted, stage of forest conversion to urban development occurred

after the Second World War from 1946–1949 (Oke et al. 1992; Macdonald 1992) (Figure 4). The

present landscape is made up of second-growth forest fragments surrounded by an urban matrix

of residential, commercial and industrial development, gardens and golf courses.
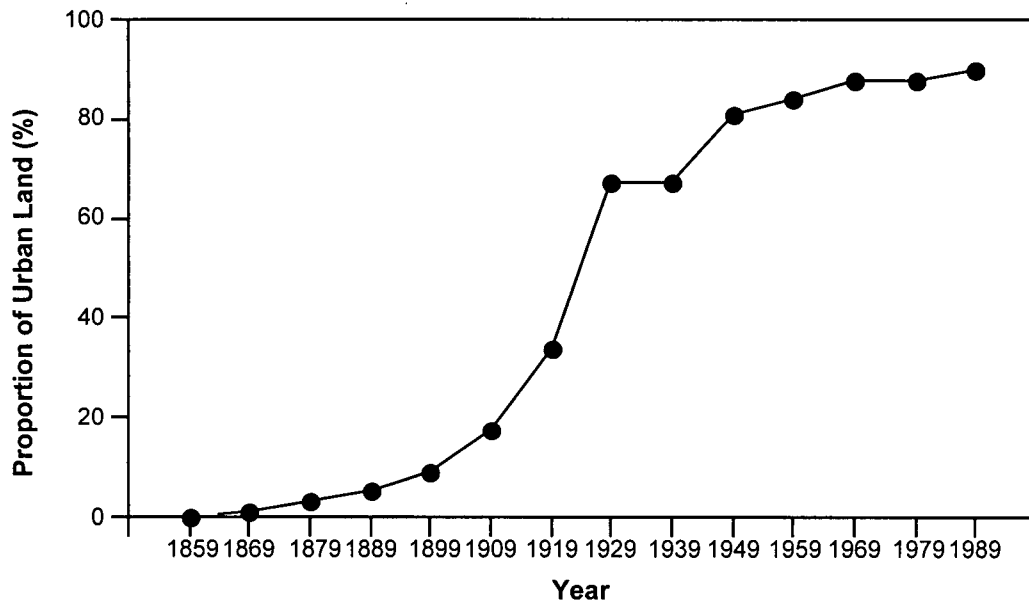
Figure 4.   Proportion of urban land in the study area (i.e. Vancouver and the lower West
Vancouver), from 1859 to 1989. Source: Macdonald (1992).

METHODS

**Testing the hypothesis that loss in forest area in the landscape with urbanization results in
bird extirpations as expressed by the species–area function**

In the first part of this study, I examined the hypothesis that the loss in forest area in the

landscape with urbanization results in bird extirpations as expressed by the species–area

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[2] A small amount of forest to the south was also converted to vegetable farming in the early 1910s, which was in
turn converted to urban development between the 1920s and 1930s (site of the present Eaglequest, Point Grey,
McCleery and Marine Drive golf courses, Southlands residential estate, and the industrial estate between Cambie
and Main to the south of SW Marine Drive).

function. The observed number of bird extirpations as a result of the loss in forest area should match that predicted by the species–area function ($S = cA^z$), if this hypothesis is correct. I used the approach of Pimm and Askins (1995) to test this prediction. The landscape represented by Vancouver was used to test this prediction. I excluded lower West Vancouver because information relating to the historical area of forest and bird species composition was incomplete.

Estimating the loss of forest area in Vancouver

The present landscape in Vancouver is made up of forest (i.e. second-growth forest) and urban development. By comparing the historical and present area of forest in Vancouver, an estimate of the loss in forest area as a result of conversion to urban development can be obtained. The historical area of forest in Vancouver was estimated from a 1859 vegetation map presented by Macdonald (1992). The digital image of this vegetation map was obtained from Dr Brian Klinkenberg (Department of Geography, University of British Columbia) and converted into a format compatible to the Geographic Information System software, ArcView GIS Version 3.2 (ESRI 1996). This involved the creation of a world file (tiffw) by calibrating the number of pixels that made up the length and width of the image to the actual distances, which was possible because the original image was scaled to actual distances. The forest cover was digitized and the area of forest estimated using ArcView. The present area of forest in Vancouver was estimated from a geometrically corrected 1999 Landsat image produced by McElhanney Land Surveys Ltd. (2000). The image was imported into ArcView, and the forest cover and area of forest was digitized and estimated. To distinguish between planted woodlots and second-growth forest in the present landscape, truthing was conducted using aerial photographs of Vancouver from 1930 and 1954. These two years were selected because they coincided with the end of the two stages of urban development in Vancouver. I excluded planted woodlots from the estimation of the present forest area in Vancouver because of interest in the loss of the historical forest area.

Determining bird species prone to extirpation as a result of the loss in forest area

To test the prediction that the observed number of bird extinctions as a result of the loss in forest area in Vancouver matched that predicted by the species–area function, I considered only bird species that would most likely become extirpated as a result of the loss in forest area. This included species closely associated with lowland temperate forests and restricted in their geographic distribution in British Columbia. A list of 243 bird species known to occur in Vancouver between 1909 and 1931 was obtained from Cumming (1932). From this list, species closely associated with lowland forests were identified according to Johnson and O'Neil (2001). Johnson and O'Neil (2001) classified species in Washington and Oregon as closely associated with a particular habitat if it was known to depend on that habitat for part or all of its life history requirements and the habitat was essential for its maintenance and viability. As the forest types and avifauna in the coastal lowlands of Washington and Oregon are relatively similar to those in the coastal lowlands of British Columbia, this database is considered applicable to the present study (Larrison et al. 1981; Pojar and MacKinnon 1994). Prior to British settlement, Vancouver was covered not only by dense coniferous forest, but consisted of deciduous forests along the coast, waterways and naturally disturbed areas. As such, bird species closely associated with lowland forests in Vancouver were identified by using Johnson and O'Neil (2001)'s classifications of "westside lowlands conifer-hardwood forests" and "westside riparian-wetlands". This resulted in a subset of 36 bird species being identified (Table 1).

Of these 36 species, two species (Spotted Owl *Strix occidentalis*, Yellow-billed Cuckoo *Coccyzus americanus*) are extirpated in Vancouver (Campbell et al. 1990a; Fraser et al. 1999). The Marbled Murrelet (*Brachyramphua marmoratus*), which nests in old-growth coniferous forests, is also believed to be extirpated (Dr Fred Cooke pers. com., 2 November 2000). Although sightings of the Marbled Murrelet are still reported off the coast of Vancouver, there has been no evidence since 1970 of the species breeding in or near the forest remaining in

19

Vancouver. From 1940–1990, there are only two records: a fledgling with egg-tooth collected at Point Grey Beach on 23 July 1941, and another fledgling with egg-tooth collected at Stanley Park on 18 July 1970 (Campbell et al. 1990a). Another two species (Great Blue Heron *Ardea herodias*, Band-tailed Pigeon *Columba fasciata*) are listed on the British Columbia Provincial Blue List and in decline in Vancouver (Campbell et al. 1990a, b; Fraser et al. 1999; B.C. Ministry of Sustainable Resource Management 2002). The Lewis' Woodpecker (*Melanerpes lewis*) and Western Bluebird (*Sialia mexicana*) were not considered here as closely associated with lowland forest in Vancouver, although they have been extirpated in Vancouver (Campbell et al. 1990a, 1997; Fraser et al. 1999). This is because they are open woodland denizens and their abundance in Vancouver from 1909–1940 can be attributed to the open areas and abundance of snags left behind after the logging of the forests (Cumming 1932; Campbell et al. 1990a, 1997).

Table 1. Bird species from Cumming's 1932 list that were identified according to Johnson and O'Neil's database as closely associated with lowland forests and the number of ecoprovinces in which they occur in British Columbia

Species	Number of Ecoprovinces
Yellow-billed Cuckoo	1
Spotted Owl	2
Marbled Murrelet	5
Western Screech-Owl *Otus kennicottii*	6
Black-throated Gray Warbler *Dendroica nigrescens*	6
Willow Flycatcher *Empidonax traillii*	7
Band-tailed Pigeon	9
Great Blue Heron	10
Wood Duck *Aix sponsa*	10
Ruffed Grouse *Bonasa umbellus*	11
Northern Saw-whet Owl *Aegolius acadicus*	11
Olive-sided Flycatcher *Contopus cooperi*	11
Pacific-slope Flycatcher *Empidonax difficilis*	11
Red-eyed Vireo	11
Warbling Vireo *Vireo gilvus*	11
Northern Rough-winged Swallow *Stelgidopteryx serripennis*	11
Mallard *Anas platyrhynchos*	12
Ring-necked Duck *Aythya collaris*	12
Harlequin Duck *Histrionicus histrionicus*	12
Hooded Merganser *Lophodytes cucullatus*	12
Common Merganser *Mergua merganser*	12
Spotted Sandpiper *Actitis macularia*	12

Table 1. Continued.

Species	Number of Ecoprovinces
Mourning Dove *Zenaida macroura*	12
Belted Kingfisher *Ceryle alcyon*	12
Downy Woodpecker *Picoides pubescens*	12
Tree Swallow *Tachycineta bicolor*	12
Cliff Swallow *Petrochelidon pyrrhonota*	12
Barn Swallow *Hirundo rustica*	12
Winter Wren *Troglodytes troglodytes*	12
Golden-crowned Kinglet	12
Varied Thrush	12
Yellow Warbler *Dendroica petechia*	12
Wilson's Warbler *Wilsonia pusilla*	12
Common Yellowthroat *Geothlypis trichas*	12
Western Tanager *Piranga ludoviciana*	12
Lincoln's Sparrow *Melospiza lincolnii*	12

From the subset of 36 bird species, species restricted in their geographic distribution in British Columbia were identified. The distribution range of these species in British Columbia was quantified by the number of ecoprovinces found within its range. This was based on distribution maps from Campbell et al. (1990a, b, 1997 and 2001a). Bird species with occurrences in ten or less ecoprovinces in British Columbia were considered to be restricted in their geographic distribution. This was arbitrary, but reflected that the majority of these 36 species could be found in 11 or 12 ecoprovinces. From this, nine species closely associated with lowland forests were deemed to be restricted in their geographic distribution (Table 1).

Predicting bird extirpations from loss in forest area

Two subsets of birds were therefore identified from Cumming's original list of bird species in Vancouver: 36 species closely associated with lowland forests and 9 species closely associated with lowland forests and restricted in their geographic distribution in British Columbia. The number of bird extirpations resulting from the loss in forest area in Vancouver was predicted for each subset of birds, as follows: $S_{new} = (A_{new}/A_{original})^z \times S_{original} \Rightarrow S_{extirpate} = S_{original}-S_{new}$, where S_{new} is the predicted number of species after forest loss and $S_{original}$ is the

original pool of species, $S_{extirpate}$ is the absolute number of extirpations, A_{new} is the area of forest remaining, $A_{original}$ is the original area of forest and z is a constant (Pimm and Askins 1995).

A z-value of 0.25 was used because the existing landscape in Vancouver is comprised of an archipelago of forest fragments (Rosenzweig 1995). This z-value is also consistent with that used by other authors (Pimm and Askins 1995; Brooks et al. 1997; Brooks et al. 1999). The sensitivity of the predictions to changes in z was tested by using values of 0.20 and 0.35. These lower and upper values were chosen because z ranges from 0.25–0.35 for an "archipelago-like" landscape and from 0.12–0.18 for nested areas within continuous forests (Rosenzweig 1995).

<u>Statistical analysis</u>

I compared the observed and predicted number of extirpations for each of the two subsets of birds. Comparison was first made against the number of bird species that were extirpated in Vancouver. Species most likely to be extirpated with time was then included to account for the time-lag between forest loss and extirpation (i.e. blue-listed species). Chi-square analysis was used to determine if differences between the observed and predicted number of extirpations were significant at $\alpha = 0.05$. This was performed with JMP Version 4.0.2 (SAS Institute 2001).

Testing the hypothesis that large fragments have greater bird species richness and densities than small fragments because large fragments contain a greater diversity and/or abundance of habitat resources

In the second part of this study, I focussed on the hypothesis that large fragments support more bird species and densities than small fragments because of greater diversity and/or abundance of habitat resources. If this hypothesis is correct, bird species richness and density would respond positively to fragment area and to habitat variables that vary positively with area. Furthermore, bird species richness and density would also not respond to habitat variables that remain constant with area. To test these predictions, field surveys were conducted to determine the bird species richness and density of several forest fragments in Vancouver and lower West

Vancouver. These were then related to fragment area, structural and floristic habitat variables that approximated the diversity and/or abundance of habitat resources in these fragments.

Study sites

A total of 14 forest fragments were selected as study sites, 13 in Vancouver and 1 in lower West Vancouver, ranging from 5–270 ha (Table 2 and Figure 5). The fragments were defined according to the protocol used by Lynch and Whigman (1984) and Askins et al. (1987). An area of forest was considered a distinct fragment if it was not interrupted by a major powerline, hard-surface roads and highway or other unforested area wider than 10 m. Hence, a forested area bisected by a road or powerline comprised two fragments. This conservative definition of fragment boundaries was essential for delineating fragments because of the system of closely adjacent forests in Vancouver. I did not use fragments less than 5 ha because the survey results would be affected by species from the surrounding landscape matrix (Haila 1988). With the exception of Lighthouse Park, which comprises "mature old forest", all the other forest fragments comprise of second-growth coastal western hemlock forest.

Table 2.   Location, area and number of transects in study sites

Study sites	Latitude, Longitude	Area (ha)	No. of bird survey transects
Brockton	49°18'03''N, 123°07'38''W	5.6	1
Campus-S	49°15'08''N, 123°14'35''W	7.8	1
16th-Uni Blvd-N	49°15'44''N, 123°14'00''W	9.1	1
Musqueam	49°13'57''N, 123°11'40''W	9.7	1
Shaughnessy	49°14'20''N, 123°12'40''W	20.1	2
W-Park Dr	49°18'26''N, 123°09'10''W	30.0	2
16th-Uni Blvd-S	49°15'34''N, 123°13'28''W	51.5	3
Uni-Chancellor Blvd	49°16'11''N, 123°14'00''W	56.7	3
E-Causeway	49°18'21''N, 123°08'28''W	63.6	3
Lighthouse	49°20'06''N, 123°15'40''W	73.5	3
N-Chancellor Blvd[a]	49°16'29''N, 123°14'00''W	98.7	3
W-Causeway	49°18'15''N, 123°09'00''W	130.2	4
S-16th Ave	49°14'45''N, 123°13'00''W	217.9	6
N-SW Marine	49°15'15''N, 123°13'00''W	265.2	7

[a] When estimating the area of N-Chancellor Blvd, I excluded areas of major ravines, which were inaccessible and impossible to survey.
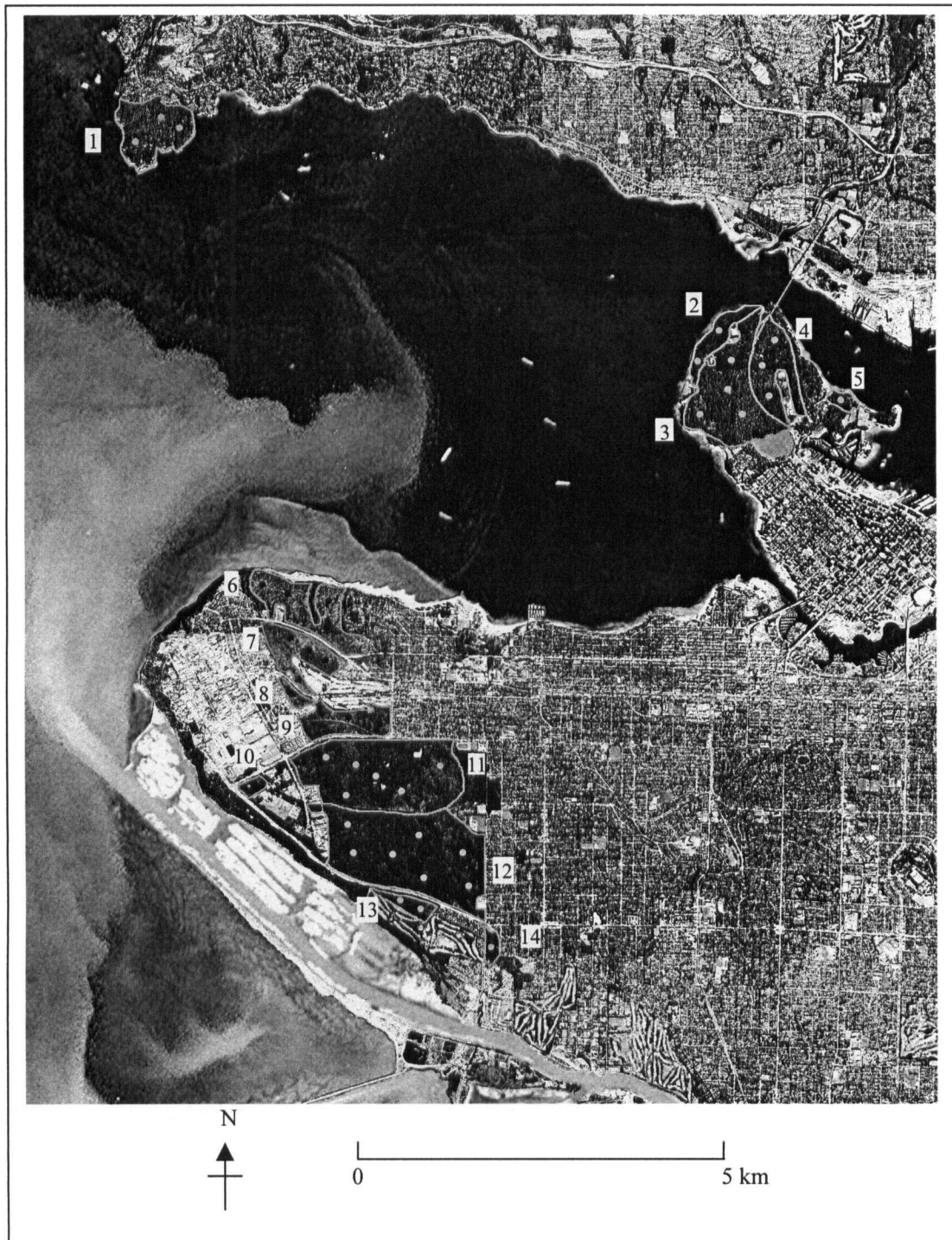
Figure 5.   Location of study sites and transects in Vancouver and lower West Vancouver.

Legend: (1) Lighthouse; (2) W-Park Dr; (3) W-Causeway; (4) E-Causeway; (5) Brockton; (6) N-Chancellor Blvd; (7) Uni-Chancellor Blvd; (8) 16th-Uni Blvd-N; (9) 16th-Uni Blvd-S; (10) Campus-S; (11) N-SW Marine; (12) S-16th Ave; (13) Shaughnessy; (14) Musqueam. Solid dots: locations of the centre of 200 m-long transects used for bird surveys. The direction of traverse and the UTM references of the transects are given in Appendix II.

<u>Bird surveys</u>

The line transect method was used to survey birds in each of these forest fragments (Emlen 1971, 1977). The line transect technique was selected because of the need in this study to replicate surveys across four seasons. During the non-breeding season, birds are less vocal and territorial (Best 1981; Skirvin 1981). Consequently, birds are less likely to be detected by the use of point counts, which rely heavily upon the detection of singing birds (Verner 1985; DeSante 1986; Bibby et al. 2000). The line transect, on the other hand, is better for detecting non-singing birds as the observer searches a larger area by moving along the transect rather than remaining stationary at a fixed point. In addition, the observer has a tendency to flush birds that would otherwise have remained undetected (Verner 1985; Bibby et al. 2000; Wilson et al. 2000).

One to seven transects, each 200 m in length, were randomly located within each fragment (total of 40 transects) (Table 2, Figure 5, Appendix II). The number of transects established in each fragment was approximately proportional to the area of the fragment. This was empirically determined through a preliminary survey conducted prior to the main study. Details of the preliminary study are presented in Appendix III. A common direction (to the nearest 22.5 degrees) was randomly selected for transects within each fragment (Buckland et al. 1993). The transects were at least 200 m apart and at least 50 m from the edge of the fragments (Bibby et al. 1992). They did not cross any forest trails. The start and end of the transects were located in the field with the help of a Garmin global positioning system. Transects were set up with a hip-chain and a prismatic compass. The centre lines of the transects were marked at 5 m intervals with red flagging tape and wherever necessary to maintain the direction of traverse. The transects were surveyed over four seasons in 2001 as follows: "spring": 23 April to 11 June; "summer": 12 June to 31 July; "fall": 16 September to 4 November; "winter": 5 November to 29 December. Each transect was surveyed twice in each season. The order in which the fragments were surveyed was randomized within each round of survey. Each round was completed within 25 days, with the

25

exception of the second round in winter. The latter took 30 days because of the longer periods of rain. The period of survey in each season was timed, as closely as possible, to coincide with the periods of migration, breeding and wintering of birds in Vancouver (Toochin 1998).

I walked along each transect at a steady pace, essentially alternating between a slow walk and brief pauses to detect and record birds (Emlen 1971, 1977). Each transect took approximately 18 minutes to survey. This survey time was empirically determined as optimal during the preliminary survey (Er et al. 2002; Appendix III). All terrestrial bird species and numbers seen or heard within 50 m of the transect were recorded (Schieck 1997). I chose to record more than singing males in this study. This is because density estimates derived from singing males tend to be biased by sex ratios that do not conform to the assumption of one female to every male (Mayfield 1981). Furthermore, replication of this study in the non-breeding seasons made the use of singing males impractical. Birds flying overhead were not recorded. Sighting angles and horizontal radial distances (from which perpendicular distances can be calculated) were estimated from all sightings and calls to the centre line of the transect. When birds occurred in flocks, distance was estimated from the centre of the flock. Distances were estimated with the aid of a laser rangefinder (distances >18 m) and a 200 mm lens fitted on a SLR camera (distances <18 m), while sighting angles were estimated with a prismatic compass. All bird detections were placed into two distance bands, 0–25 m and 25–50 m (Jarvinen and Vaisanen 1975; Buckland et al. 1993; Bibby et al. 2000). All surveys were conducted within 4 hours of sunrise in spring and summer, and within 3 hours of sunrise in fall and winter (Robbins 1981a; Gutzwiller 1991). Surveys were conducted when it was not raining and when the wind speed did not exceed 25 km/h (Robbins 1981b). Surveys were not conducted during the few days of snow in winter, and re-commenced only after all the snow on the ground had melted.

The survey data were filtered prior to any subsequent calculations or analysis. Firstly, strictly transient species were excluded from the summer and winter data. Transient species refer

to species that do not breed or winter in the study area. These species were identified according to Toochin (1998) and Campbell et al. (2001b). Secondly, observations of owls were excluded because the survey methodology was not catered towards this group of birds. Finally, species with only one detection within each season were excluded. This ensured that only species that were probably using the forest fragments were analyzed. I also assumed that the observations in each season were representative of the known seasonal activity of birds in the study area.

Bird species richness for each fragment was calculated as the cumulative number of bird species detected during the surveys. This was enumerated separately for each season. Overall bird density was estimated for each transect within the two distance bands by assuming that the detectability of birds varied according to a half-normal distribution with distance from the centre line (Jarvinen and Vaisanen 1975; O'Meara 1981; Buckland et al. 1993; Bibby et al. 2000). This is as follows: $\hat{D} = \dfrac{10^3 N}{T\sigma\sqrt{2\Pi}} \times \dfrac{1}{100}$,where $\hat{D}$ is the estimated relative bird density (birds/ha), N is the total number of bird detections (filtered), T is the total length of the transect (km) and σ is the standard deviation of a normal distribution with mean $\mu=0$. Hence, $\sigma = w/z$, where w is the distance from the centre line to the first distance band and z is the normal deviate, which can be obtained from the proportion of total bird detections found within the first distance band (Jarvinen and Vaisanen 1975). The bird density in each transect was estimated for each round of survey. This was then averaged over the two surveys in each season. A mean density was obtained for fragments in each season by averaging the densities over all transects in the fragment (for fragments with only one transect, this was the density of that transect averaged over the two surveys in each season).

The bird species observed in the surveys were further classified according to their seasonal status in Vancouver (residents or migrants), and according to their foraging guilds by diet (insectivores or granivores) and by foraging techniques (foliage gleaners, ground gleaners, bark

27

gleaners and hawkers) (Appendix IV). Residents refer to species that occur throughout the year, while migrants refer to species that occur only either in summer or winter in the Vancouver region (Toochin 1998; Campbell et al. 2001b). Species that comprise of different populations (e.g. American Robin *Turdus migratorius*) and those that move between low and high elevational sites within the Vancouver region (e.g. Varied Thrush) during the breeding and non-breeding seasons would be classified as residents. The advantage of this set of definitions is that it clearly delineates species that visit the Vancouver region only in certain times of the year. The classification into various foraging guilds by diet and foraging techniques followed Ehrlich et al. (1988). The densities of each of these functional groups were calculated for each fragment in each season in the same manner as for overall bird density. The use of functional groups facilitates the assessment of the effects of changes in habitat resources because such groupings are centred upon the type of resources utilized by species (Landres 1983; Verner 1984).

Habitat sampling

Habitat variables were sampled within each of the bird survey transects according to the protocol developed by James and Shugart (1970) for the quantification of bird habitats. This involved the use of 0.04 ha circular plots and 20 m^2 (20 m x 1 m) belt transects. Habitat sampling was focussed only in the area where birds were surveyed, i.e. 200 m by 100 m of the bird survey transect. Each transect was sub-divided into four equal strata (Anderson and Ohmart 1986). Within each stratum, a circular plot was randomly located. Hence, a total of four circular plots were established within each transect. Within each circular plot, two perpendicular belt transects (20 m by 1 m) were randomly established across the centre of the plot. Along each of these 20m-transects, sampling points were established at 2 m-intervals. A total of 20 sampling points were therefore established within each circular plot (Figure 6). Habitat sampling was done by three persons (Kenneth Er and two field assistants), from 6 July–8 August 2001.

200 m–long bird survey transect

4 x circular plots (0.04 ha, 11.28 m radius)
2 x perpendicular belt transects (20 x 1 m), with 10
sampling points at 2 m intervals.
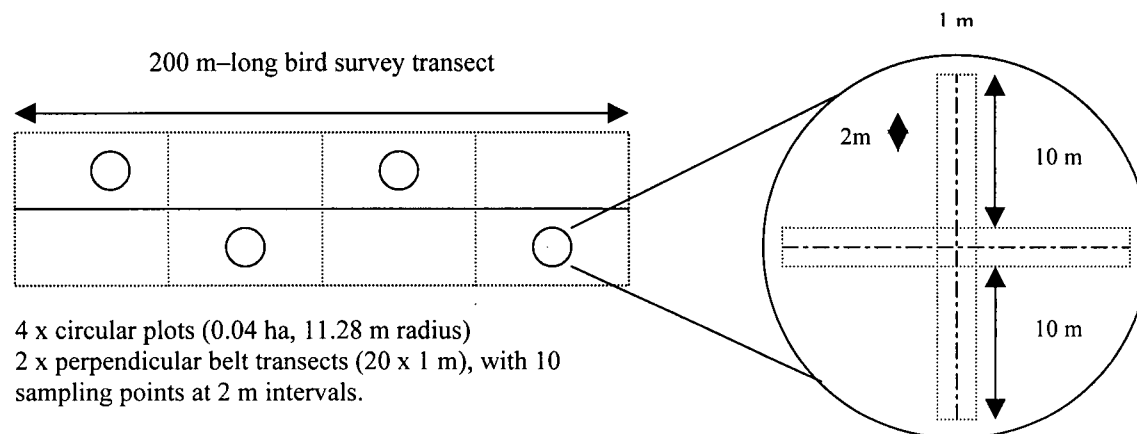
Figure 6.   Plot design for habitat sampling.

Within each of the circular plots, all trees with a diameter at breast height greater than 12.7 cm and a height of at least 5 m were enumerated (USDA Forest Service 1998). I gauged whether trees were in or out of the plot by estimating the distance between the tree and the centre of the plot with a 200 mm lens fitted on a SLR camera. The species, diameter at breast height and tree condition were recorded. Tree condition was scored visually according to the decay stages presented by McComb and Lindenmayer (1999). Trees with higher scores were in later decay stages (Figure 7). Shrubs of all species (including saplings) between 0.5–5 m in height were enumerated within each of the 20 x 1 m-transect belts (USDA Forest Service 1998). A 0.5 m-long stick was used to gauge whether the shrubs were within 0.5 m of the transect.

At each sampling point along the 20 m-long transects, the presence or absence of foliage cover within a circle of 0.5 m diameter was recorded at the following heights: 0m, 0.5m, 1m, 3m, 5m, 10m, 15m, 20m, 25m, 30m, 35m, 40m, and >40 m. These height intervals were similar to those used in Douglas-fir forests in Oregon (Mannan and Meslow 1984). Presence of foliage at the various heights was determined by the interception of foliage by a graduated pole (for heights up to 5 m) and the line of sight of a standard 200 mm lens attached to a 35mm SLR camera pointing vertically upwards (for heights greater than 5 m) (Erdelen 1984). Distances corresponding to the height intervals (up to 40 m) were calibrated on the focussing scale of the

200 mm lens, taking into account the distance of the camera from the ground (approximately 1.5 m). Calibration of the lens to the various distances was done by focussing on a pole placed at fixed horizontal ground distances from the camera. Distances were set up with a measuring tape.
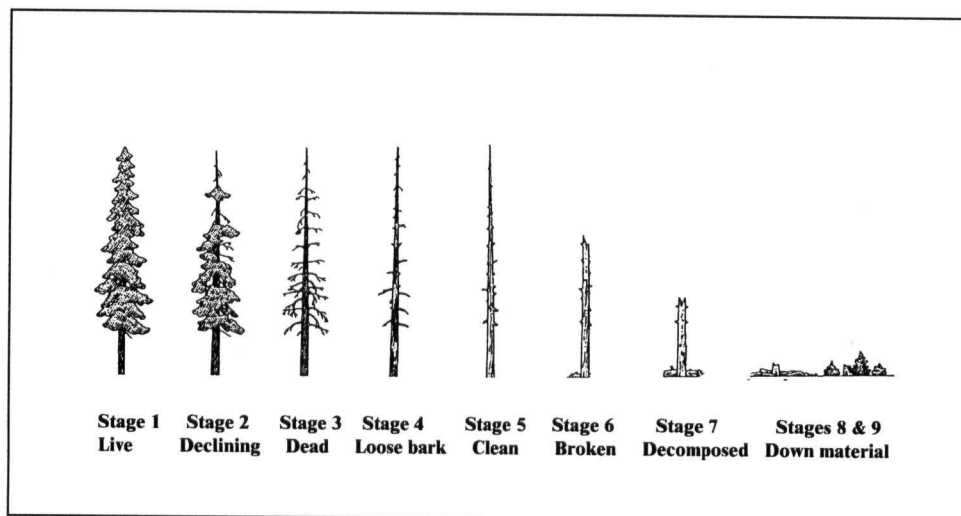
Figure 7.   Decay stages used to score the condition of trees. Source: McComb and Lindenmayer (1999).

A tree in decay stage 1 was given a score of 1, while a tree in decay stage 6 was given a score of 6. The decay stages were also applied to deciduous broadleaved trees, using the same definitions that accompanied each of the stages.

Using the data derived from the habitat sampling, 13 habitat variables were calculated for each of the bird survey transects (Table 3). This included tree species diversity, proportion of deciduous broadleaved trees, proportion of coniferous trees, mean tree diameter, tree density, mean tree condition, shrub density, shrub species diversity, proportion of understorey foliage cover (<5 m), proportion of overstorey foliage cover (>10 m), total foliage cover, foliage height diversity and horizontal heterogeneity. These variables were then averaged across all the transects within each forest fragment (for fragments with only one transect, this was the value of the habitat variables calculated for that transect).

Table 3.　Method of calculating the habitat variables for each bird survey transect

Habitat variables	Method of calculation
Proportion of coniferous trees (Conifer)	Number of coniferous trees, as a proportion of the total number of trees enumerated in all four circular plots.
Proportion of deciduous broadleaved trees (Decid)	Number of deciduous broadleaved trees, as a proportion of the total number of trees enumerated in all four circular plots.
Tree species diversity (TSD)	Shannon-Wiener diversity index (H), calculated by using all trees enumerated from all four circular plots as follows: $H = -\sum P_i \ln (P_i)$, where P_i is the proportion of individuals found in the ith species (Magurran 1988).
Mean diameter at breast height (DBH)	Mean of the diameter at breast height of all trees enumerated from all four circular plots.
Tree density (TrDen)	Number of trees per hectare, calculated from all trees enumerated from all four circular plots.
Mean tree condition (MTCond)	Mean of the condition (decay) score of all trees enumerated from all four circular plots.
Shrub density (ShDen)	Number of shrubs per hectare, calculated from all shrubs enumerated from all eight belt transects.
Shrub species diversity (ShSD)	Shannon-Wiener diversity index (H), calculated by using all shrubs enumerated from all eight belt transects as follows: $H = -\sum P_i \ln (P_i)$, where P_i is the proportion of individuals found in the ith species (Magurran 1988).
Proportion of understorey foliage cover (UnCov)	Number of times foliage was intercepted, as a proportion of the total number of samples for all sampling points and height intervals ≤ 5 m.
Proportion of overstorey foliage cover (OvCov)	Number of times foliage was intercepted, as a proportion of the total number of samples for all sampling points and height intervals >10 m.
Total foliage cover (TotCov)	The foliage profile was divided into seven layers: 0-0.5 m, 0.51-3.0 m, 3.01-10.0 m, 10.01-20.0m, 20.01-30.0 m, 30.01-40.0 m, >40.0m. Proportion of foliage in each layer was calculated as the number of times foliage was intercepted, as a proportion of the total number of samples for all sampling points and height intervals within the layer. Total foliage cover was the sum of these proportions for all seven layers (Anderson and Ohmart 1986).
Foliage height diversity (FHD)	Shannon-Wiener diversity index (H), calculated as follows: $H = -\sum P_i \ln (P_i)$, where P_i is the proportion of foliage found in the ith layer, using all seven layers described previously (Erdelen 1984; Anderson and Ohmart 1986).
Horizontal heterogeneity (HH)	The proportion of foliage in each layer was calculated as the number of times foliage was intercepted, as a proportion of all sampling points and height intervals within the layer, for each circular plot. The statistical variance of the proportion of foliage in each layer was calculated across all four circular plots. Horizontal heterogeneity was the sum of these variances for all seven foliage layers (Anderson and Ohmart 1986).

<u>Statistical analysis</u>

I first constructed a pairwise correlation matrix comprising of all the habitat variables. Auto-correlated variables were identified and factored into the interpretation of subsequent analysis involving these variables. I also ascertained the relationships between the habitat variables and fragment area using simple linear regression. From here, habitat variables that varied positively with area and those that remained constant with area were identified.

I then proceeded to test the prediction that bird species richness would respond positively to fragment area and to habitat variables that varied positively with area, after correcting for the effects of sampling effort. The species–area function, $S = cA^z$, was fitted to bird species richness data obtained from the survey of the fragments using non-linear regression. Gauss-Newton search algorithms were used to obtain global estimates of the constants, c and z (Neter et al. 1996). A goodness of fit was determined by calculating the coefficient of determination (R^2) and an F-statistic from the corrected total sum of squares (SAS Institute 1999). Rarefaction was then used to correct for sampling effort. This involved calculating an expected number of species corresponding to a standardized number of individuals for each fragment, as follows:

$$E(S) = \sum \left\{ 1 - \left[\binom{N - N_i}{n} \middle/ \binom{N}{n} \right] \right\}$$,where E(S) is the expected number of species or known

here as the rarefied bird species richness, n is the standardized sample size (i.e. the number of individuals in the smallest sample), N is the total number of individuals recorded, and N_i is the number of individuals in the ith species (Magurran 1988). The species–area function was re-fitted to the rarefied data. Obtaining statistically similar fits with the original and rarefied datasets would suggest that sampling effort did not have an adverse effect on the relationship between bird species richness and fragment area. Finally, I fitted rarefied bird species richness against the habitat variables that varied positively with area using simple linear regression.

Next, I tested the prediction that bird species richness would not respond to habitat variables that remained constant with area, after correcting for the effects of sampling. Simple linear regression was used to fit rarefied bird species richness against habitat variables that remained constant with area. Where habitat variables that varied positively with area and those that remained constant with area were found to significantly influence rarefied bird species richness, I determined if the latter group of habitat variables would add significantly to the variation in rarefied bird species richness as explained by the former group of habitat variables. This was done using multiple linear regression, with the "forward stepwise"[3] procedure.

Using simple linear regression, I also tested the predictions that overall bird density and density of various functional groups of birds would respond positively to fragment area, and to habitat variables that varied with area. I further tested the prediction that they would not respond to habitat variables that remained constant with area. Multiple linear regression was used in the same manner as with rarefied species richness, when habitat variables that varied positively with area and those that remained constant with area were equally influential on density.

All analyses were conducted independently for each season. In all analyses involving simple and multiple regression, residual and normality plots were used to detect departures from constant variance, normality and lack of linear fit. Where necessary, a natural logarithmic transformation was applied to the independent variables to ensure normality and to correct for the lack of linear fit (Neter et al. 1996). Acceptance of all models was taken at significance level $\alpha = 0.05$ (i.e. $p < 0.05$). SAS Version 8.0 (SAS Institute 1999) was used to perform the non-linear regressions, while JMP Version 4.0.2 (SAS Institute 2001) was used for all other analysis.

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[3] The multiple regression models were also fitted using the "backward elimination" procedure. The results did not differ from that obtained by the "forward stepwise" procedure due to the small number of variables involved. As such, only results from the "forward stepwise" procedure are reported here. The "forward stepwise" procedure is also more aligned to my intent of determining if habitat variables that remained constant with area added to the variation in bird species richness or density as explained by habitat variables that varied positively with area.

CHAPTER 3

RESULTS

MATCHING OBSERVED NUMBER OF BIRD EXTIRPATIONS TO THAT PREDICTED FROM THE SPECIES–AREA FUNCTION

From the 1859 vegetation map and the geometrically corrected 1999 Landsat image, the area of forest in Vancouver was estimated to be approximately 11630 ha in 1859, compared to 1536 ha in 1999. In 1999, 13% of the original area of forest in 1859 remained (Figure 8).

(a)   (b)
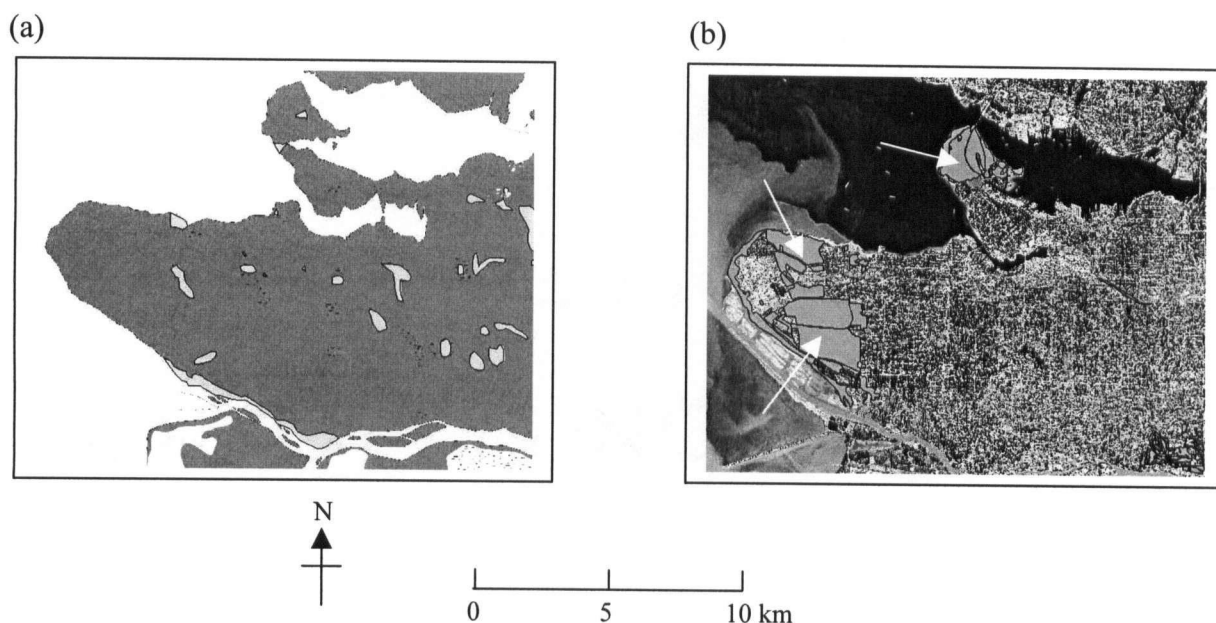
Figure 8.   Forest cover (indicated by arrows) of Vancouver in (a) 1859 and (b) 1999.

Using the subset of 36 bird species closely associated with lowland forests in Vancouver as the original pool of species (i.e. $S_{original}$), 0.13 as the value of $A_{new}/A_{original}$ and 0.25 as the value of z, 14 bird species were predicted from the species–area function as likely to be extirpated as a result of the loss in forest area. This prediction was significantly higher than the observed number of bird extirpations in Vancouver ($p < 0.05$, Table 4). Of these 36 species, only three are extirpated in Vancouver (Spotted Owl, Yellow-billed Cuckoo and Marbled Murrelet). By restricting the comparison to the subset of nine species closely associated with lowland forests in

34

Vancouver and restricted in their geographic distribution in British Columbia (i.e. $S_{original} = 9$), four species were predicted as likely to be extirpated. This prediction was close to the three species (of this subset of nine species) known to be extirpated (Spotted Owl, Yellow-billed Cuckoo and Marbled Murrelet, Table 4). Hence, the observed number of bird extirpations matched closely that predicted by the species–area function only with species closely associated with lowland forests and restricted in their geographic distribution.

Interpretation of these results is contingent on the value of z and hence the sensitivity of the species–area function to the variation in z. The number of bird extirpations was predicted using the z-values of 0.20 and 0.35 for both subsets of birds (i.e. those closely associated with lowland forests, and those closely associated with lowland forests and restricted in their geographic distribution). In both cases, the predicted number of bird extirpations increased with z. However, this did not change the overall conclusions obtained from comparing the observed and predicted number of extirpations with a z-value of 0.25 (Table 4).

Taking into account the time-lag between forest loss and extirpation, two other species found within the two respective subsets of birds were considered as most likely to be extirpated with time. These species, namely the Great Blue Heron and Band-tailed Pigeon, are on the British Columbia Provincial Blue list (B.C. Ministry of Sustainable Resource Management 2002). For both subsets of birds, inclusion of these species as "extirpated" increased the observed number of extirpations to five. For the subset of species closely associated with lowland forests, the observed number of extirpations was still significantly lower than the predicted number of extirpations ($p < 0.05$, Table 4). On the other hand, for the subset of species closely associated with lowland forests and restricted in their geographic distribution, the observed number of extirpations became higher than the predicted number of extirpations. However, this difference was not significant ($p > 0.05$, Table 4).

Table 4. Comparison of observed and predicted number of bird extirpations as a result of forest loss in Vancouver

z-value	$S_{original}$	Observed number of extirpations[a]	Predicted number of extirpations	χ^2_1	p-value
Species closely associated with lowland forests					
0.20	36	3 (8%)	12 (33%)	10.13*	< 0.001
0.25	**36**	**3 (8%)**	**14 (39%)**	**14.14***	**< 0.001**
0.35	36	3 (8%)	18 (50%)	25.00*	< 0.001
Species closely associated with lowland forests and restricted in their geographic distribution					
0.20	9	3 (33%)	3 (33%)	0	p = 1.000
0.25	**9**	**3 (33%)**	**4 (44%)**	**0.45**	**p = 0.200**
0.35	9	3 (33%)	5 (55%)	1.80	p = 0.140
Accounting for time-lag in extirpation: Species closely associated with lowland forests					
0.25	36	5 (14%)	14 (39%)	9.47*	p < 0.001
Species closely associated with lowland forests and restricted in their geographic distribution					
0.25	9	5 (55%)	4 (44%)	0.45	p = 0.200

[a]Extirpated species include the Spotted Owl, Yellow-billed Cuckoo and Marbled Murrelet; likely to be extirpated species include the Great Blue Heron and Band-tailed Pigeon. * Significant at $\alpha = 0.05$.

RELATING GREATER BIRD SPECIES RICHNESS AND DENSITIES IN LARGER FRAGMENTS TO THE DIVERSITY AND/OR ABUNDANCE OF HABITAT RESOURCES

Seasonal trends in bird species richness and density

A total of 4945 detections of 52 bird species were recorded during the transect surveys (Appendices V and VI). The data filtering process excluded 4 species and 21 detections from the analysis. This included observations of transient species (Yellow-rumped Warbler *Dendroica coronata*, Townsend's Warbler *Dendroica townsendi* and MacGilivray's Warbler *Oporornis tolmiei* in summer, and Ruby-crowned Kinglet *Regulus calendula* in winter), Barred Owl (*Strix varia*) in spring, summer and winter, and species with one detection in each season (Black-headed Grosbeak *Pheucticus ludovicianus*, Common Raven *Corvus corax*, White-crowned Sparrow *Zonotrichia albicollis* and Willow Flycatcher in spring, Common Raven and Bushtit *Psaltriparus minimus* in summer, and Common Raven in Fall).

36

Across the seasons, the number of bird species detected was highest in spring (42 species) and lowest in winter (23 species). The number of bird species detected in summer and fall were about the same and intermediate between spring and winter (32 species in summer and 31 species in fall) (Figure 9). These seasonal differences in bird species number could be attributed to the number of migrant species. In spring, return of migrants from the neotropics resulted in the detection of 17 migrant species. Of these 17 species, 12 species continued to be detected during summer, suggesting that some migrant species were breeding in the forest fragments. In fall, migration occurs over a protracted period at the end of August and a longer period from mid-September to mid-October (Toochin 1998; Campbell et al. 2001b). By the end of August, some migrant species had departed from the study area, including some of the thrushes (e.g. Swainson's Thrush *Catharus ustulatus* and Hermit Thrush *Catharus guttatus*), vireos (e.g. Warbling and Red-eyed Vireo) and flycatchers (e.g. Pacific-slope and Hammond's Flycatcher *Empidonax hammondii*). These species were not detected in the fall survey. The Fox Sparrow (*Passerella iliaca*) was the only migrant detected in winter. In contrast to the migrant species, the number of resident species was stable across the seasons (20 to 23 species, Figure 9).

Overall bird density across all transects averaged 9.1 birds/ha in spring, 6.4 birds/ha in summer, 9.6 birds/ha in fall and 8.5 birds/ha in winter (Figure 9). The high density in spring and fall reflects the increased numbers of migrant species in the study area. In addition, the high density in fall was due to the detection of large flocks of resident species such as the Golden-crowned Kinglet, the Chestnut-backed Chickadee (*Poecile rufescens*), Black-capped Chickadee (*Poecile atricapillus*) and Pine Siskin (*Carduelis pinus*). Overall, the seasonal density trends showed that the periods of survey were well delineated according to seasonal bird activity. Densities for surveys within each season did not differ significantly (i.e. overlapping standard error bars). Furthermore, the standard errors in fall and winter were greater than in spring and summer, reflecting the presence of flocks in fall and winter (Figure 9).
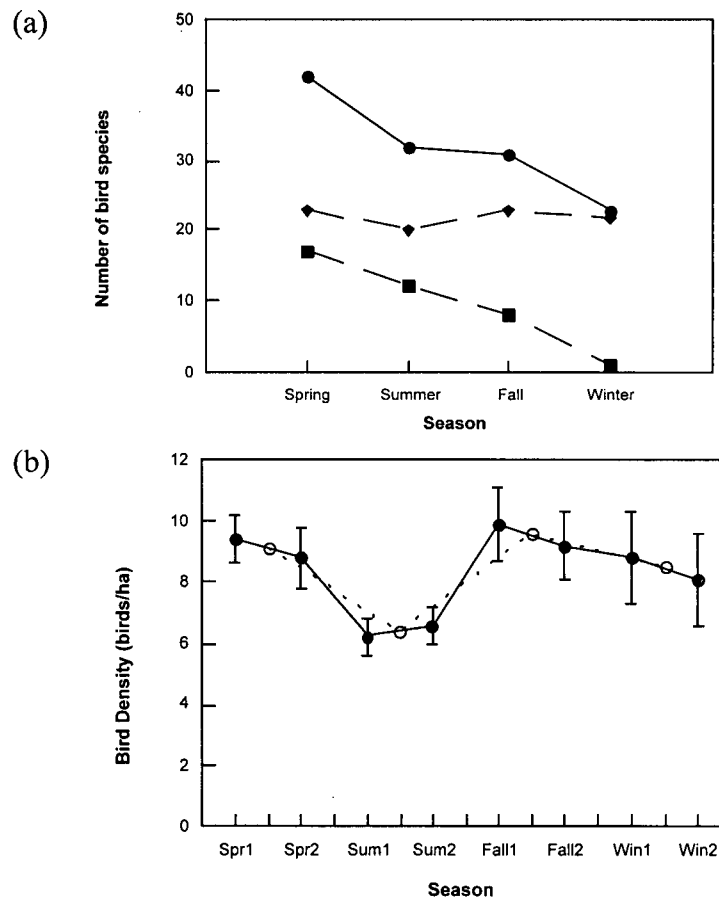
Figure 9. Seasonal trends of (a) total number of bird species (circle), resident species (diamond) and migrant species (square); (b) mean bird density across survey rounds (filled circle) and across each season (open circle).

Tabulating the number of detections for each species by season revealed that the most common species in all functional groups were largely the same in fall and winter. Seasonal changes in species that were most commonly detected were observed amongst the residents, migrants, insectivores and foliage gleaners. Amongst the residents and insectivores, the Winter Wren was most common in spring, while the Chestnut-backed Chickadee and Golden-crowned Kinglet were most common in summer and fall/winter respectively. The Wilson's Warbler was the most common migrant in spring, but was surpassed by the Swainson's Thrush and Ruby-crowned Kinglet in summer and fall respectively. The Golden-crowned Kinglet was also the most commonly detected foliage gleaner in fall/winter, but not in spring/summer. Across the seasons, the Pine Siskin was the most common granivore; the Winter Wren and Spotted Towhee

38

(*Pipilo maculatus*) were the most common ground gleaners; the Brown Creeper (*Certhia americana*) and Red-breasted Nuthatch (*Sitta canadensis*) were the most common bark gleaners; and the Pacific-slope Flycatcher was the most common hawker (Table 5).

Table 5. The four most common species in each functional bird group across seasons

Spring Species	No.	Summer Species	No.	Fall Species	No.	Winter Species	No.
Residents							
Winter Wren	214	Chestnut-backed Chickadee	172	Golden-crowned Kinglet	366	Golden-crowned Kinglet	413
Black-capped Chickadee	104	Winter Wren	150	Winter Wren	208	Winter Wren	198
Chestnut-backed Chickadee	93	Spotted Towhee	100	Chestnut-backed Chickadee	201	Chestnut-backed Chickadee	151
Golden-crowned Kinglet	86	Black-capped Chickadee	99	Black-capped Chickadee	161	Black-capped Chickadee	150
Migrants							
Wilson's Warbler	41	Swainson's Thrush	88	Ruby-crowned Kinglet	62	Fox Sparrow	7
Pacific-slope Flycatcher	38	Pacific-slope Flycatcher	54	Yellow-rumped Warbler	51		
Swainson's Thrush	36	Wilson's Warbler	24	Wilson's Warbler	28		
Yellow-rumped Warbler	31	Warbling Vireo	16	Fox Sparrow	7		
Insectivores							
Winter Wren	214	Chestnut-backed Chickadee	172	Golden-crowned Kinglet	366	Golden-crowned Kinglet	413
Black-capped Chickadee	104	Winter Wren	150	Winter Wren	208	Winter Wren	198
Chestnut-backed Chickadee	93	Spotted Towhee	100	Chestnut-backed Chickadee	201	Chestnut-backed Chickadee	151
Golden-crowned Kinglet	86	Black-capped Chickadee	99	Black-capped Chickadee	161	Black-capped Chickadee	150
Granivores							
Pine Siskin	27	Pine Siskin	24	Pine Siskin	70	Pine Siskin	143
Dark-eyed Junco *Junco hyemalis*	13	Purple Finch	4	Dark-eyed Junco	18	Dark-eyed Junco	23
Purple Finch *Carpodacus purpureus*	9	Dark-eyed Junco	2	Evening Grosbeak *Coccothraustes vespertinus*	8	Evening Grosbeak	4
Evening Grosbeak	2			Purple Finch	5	Purple Finch	3

Table 5. Continued.

Spring Species	No.	Summer Species	No.	Fall Species	No.	Winter Species	No.
Foliage gleaners							
Black-capped Chickadee	104	Chestnut-backed Chickadee	172	Golden-crowned Kinglet	366	Golden-crowned Kinglet	413
Chestnut-backed Chickadee	93	Black-capped Chickadee	99	Chestnut-backed Chickadee	201	Chestnut-backed Chickadee	151
Golden-crowned Kinglet	86	Swainson's Thrush	88	Black-capped Chickadee	161	Black-capped Chickadee	150
Wilson's Warbler	41	Wilson's Warbler	24	Pine Siskin	70	Pine Siskin	143
		Pine Siskin	24				
Ground gleaners							
Winter Wren	214	Winter Wren	150	Winter Wren	208	Winter Wren	198
Spotted Towhee	79	Spotted Towhee	100	Spotted Towhee	61	Spotted Towhee	53
American Robin	55	American Robin	36	Northwestern Crow Corvus caurinus	46	Northwestern Crow	31
Northwestern Crow	48	Northwestern Crow	33	Varied Thrush	21	American Robin	28
Bark gleaners							
Brown Creeper	34	Brown Creeper	44	Brown Creeper	47	Brown Creeper	41
Red-breasted Nuthatch	27	Red-breasted Nuthatch	22	Northern Flicker Colaptes auratus	37	Northern Flicker	11
Downy Woodpecker	12	Hairy Woodpecker Picoides villosus	18	Red-breasted Nuthatch	29	Red-breasted Nuthatch	11
Pileated Woodpecker Dryocopus pileatus	8	Downy Woodpecker	11	Hairy Woodpecker	16	Hairy Woodpecker	10
Hawkers							
Pacific-slope Flycatcher	38	Pacific-slope Flycatcher	54	Absent		Absent	
Hammond's Flycatcher	8	Olive-sided Flycatcher	2				
Olive-sided Flycatcher	3						

Correlation between habitat variables and relating habitat variables to fragment area

The survey of habitat variables revealed that these fragments comprised a mix of coniferous and deciduous broadleaved trees in various proportions (i.e. Douglas-fir, western

hemlock, western redcedar, red alder and bigleaf maple). The proportion of coniferous trees ranged from 0.18–0.90, with N-Chancellor Blvd being predominantly deciduous and Lighthouse being predominantly coniferous. The proportion of understorey foliage cover was generally high (greater than 0.45 in all fragments, except Brockton and Lighthouse) (Appendix VII).

Pairwise correlation matrix of habitat variables revealed several patterns (Table 6). Forest fragments with a high proportion of coniferous trees[4] had greater mean tree diameter, compared to fragments with high proportions of deciduous broadleaved trees. Conifer-dominated fragments also had lower tree density and shrub density than deciduous broadleaved-dominated fragments. Fragments with high tree species diversity also had high total foliage cover and shrub species diversity. High total foliage cover was in turn associated with high proportion of understorey foliage cover, the latter being positively correlated with shrub species diversity ($p < 0.05$). Tree species diversity was positively correlated with the proportion of deciduous broadleaved trees ($p < 0.1$). Although not significant at $\alpha = 0.05$, it suggests that deciduous broadleaved trees contributed partly to high tree species diversity.

Simple linear regression between habitat variables and fragment area delineated the habitat variables into those that varied with area and those that did not. The analysis revealed that tree species diversity, mean tree condition and proportion of overstorey foliage cover varied positively with fragment area ($p < 0.05$, Table 7).

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[4] The proportion of deciduous broadleaved trees and proportion of coniferous trees would add up to 1 in all fragments, except Lighthouse. This is because of the presence of *Arbutus menziesii*, which is an evergreen broadleaved tree. Correlations relating to these variables would inevitably be the same, but in opposite directions. However, both variables are presented here for the purpose of clarity and discussion.

Table 6.   Pairwise correlation matrix of habitat variables

	Conifer	Decid	TSD	DBH	TrDen	MTCond	ShDen	ShSD	UnCov	OvCov	TotCov	FHD	HH
Conifer	-	-1.00*	-0.47	0.54*	-0.41	-0.10	-0.51	-0.32	-0.48	0.06	-0.38	0.26	0.22
Decid	-1.00*	-	0.47	-0.54*	0.41	0.10	0.51	0.32	0.48	-0.06	0.38	-0.26	-0.22
TSD	-0.47	0.47	-	0.07	0.29	0.53	-0.06	0.56*	0.46	0.53	0.65*	0.27	-0.27
DBH	0.54*	-0.54*	0.07	-	-0.74*	-0.09	-0.70*	-0.10	-0.22	0.16	-0.13	0.25	-0.10
TreeDen	-0.41	0.41	0.29	-0.74*	-	0.52	0.38	0.61*	0.41	0.17	0.43	0.01	-0.19
MTCond	-0.10	0.10	0.53	-0.09	0.52	-	-0.15	0.41	0.04	0.35	0.18	-0.02	-0.24
ShDen	-0.51	0.51	-0.06	-0.70*	0.38	-0.15	-	0.17	0.26	-0.30	0.08	-0.05	0.15
ShSD	-0.32	0.32	0.56*	-0.10	0.61*	0.41	0.17	-	0.71*	0.25	0.71*	0.33	-0.22
UnderCov	-0.48	0.48	0.46	-0.22	0.41	0.04	0.26	0.71*	-	0.06	0.89*	-0.09	-0.20
OverCov	0.06	-0.06	0.53	0.16	0.17	0.35	-0.30	0.25	0.06	-	0.49	0.35	0.27
TotCov	-0.38	0.38	0.65*	-0.13	0.43	0.18	0.08	0.71*	0.89*	0.49	-	0.11	-0.07
FHD	0.26	-0.26	0.27	0.25	0.01	-0.02	-0.05	0.33	-0.09	0.35	0.11	-	0.03
HH	0.22	-0.22	-0.27	-0.10	-0.19	-0.24	0.15	-0.22	-0.20	0.27	-0.07	0.03	-

Values refer to the correlation coefficient (r). Conifer: proportion of coniferous trees; Decid: proportion of deciduous broadleaved trees; TSD: tree species diversity; DBH: mean tree diameter at breast height; TrDen: tree density; MTCond: mean tree condition; ShDen: shrub density; ShSD: shrub species diversity; UnCov: proportion of understorey foliage cover; OvCov: proportion of overstorey foliage cover; TotCov: total foliage cover; FHD: foliage height diversity; HH: horizontal heterogeneity.

* significant at $\alpha = 0.05$.

42

Table 7. Relating habitat variables to fragment area using simple linear regression

Habitat variables	R^2	$F_{1,12}$	p-value
Proportion of coniferous trees (Conifer)	0.03	0.41	0.533
Proportion of deciduous broadleaved trees (Decid)	0.03	0.41	0.534
Tree species diversity (TSD)[a] (+)	**0.45**	9.99*	0.008
Mean tree diameter at breast height (DBH)	0.05	0.62	0.445
Tree density (TrDen)	0.02	0.27	0.613
Mean tree condition (MTCond)[a] (+)	**0.30**	5.03*	0.045
Shrub density (ShDen)	0.02	0.29	0.598
Shrub species diversity (ShSD)	0.03	0.31	0.584
Proportion of understorey foliage cover (UnCov)	0.01	0.07	0.790
Proportion of overstorey foliage cover (OvCov)[a] (+)	**0.48**	10.91*	0.006
Total foliage cover (TotCov)	0.04	0.54	0.478
Foliage height diversity (FHD)	0.07	0.96	0.345
Horizontal heterogeneity (HH)	0.01	0.09	0.767

[a] Natural logarithmic transformation applied to area to correct for non-linearity. (+) positive relationship, indicated only for relationships that are significant at $\alpha = 0.05$. * significant at $\alpha = 0.05$.

Prediction: Bird species richness in forest fragments responds positively to fragment area, and to the diversity and/or abundance of habitat resources that vary positively with area, after correcting for the effects of sampling effort

In all seasons, a significant fit was obtained between bird species richness and fragment area with the power function, $S = cA^z$, by using non-linear regression ($p < 0.05$, Table 8; Figure 10). The z-value for the species–area functions ranged from 0.28–0.31, within the range expected for a landscape resembling an archipelago of islands (Rosenzweig 1995). Although the species–area fits suggest that large fragments supported more species than small fragments, the larger fragments were also sampled with greater effort (i.e. more transects) in this study. Using rarefaction to standardize the sampling effort, an expected number of bird species was calculated for each fragment in each season. Re-fitting the power function to the rarefied data revealed that rarefied bird species richness increased significantly in spring, summer and fall, but not in winter ($p < 0.05$, Table 8, Figure 10). The results suggest that the bird species–area relationship could be a biologically-based pattern in spring, summer and fall, but an artefact of sampling in winter.

Regressing rarefied bird species richness against habitat variables that varied positively with fragment area (i.e. tree species diversity, mean tree condition and the proportion of

43

overstorey foliage cover) revealed that rarefied bird species richness increased significantly with tree species diversity in spring, summer and fall; mean tree condition in summer and fall; and the proportion of overstorey foliage cover in spring and fall ($p < 0.05$, Table 9). Rarefied bird species richness did not respond significantly to the three habitat variables in winter ($p > 0.05$, Table 9). Where bird species richness varied positively with fragment area, a similar positive response was also observed with habitat variables that varied positively with fragment area, after correcting for sampling effort.

Table 8. Bird species richness and rarefied bird species richness in relation to fragment area across seasons

	Spring	Summer	Fall	Winter
Species–Area	$S = 5.83 \, Area^{0.31}$ $R^2 = 0.89$ $F_{1,12} = 98.27*$ $p < 0.001$	$S = 4.74 \, Area^{0.28}$ $R^2 = 0.89$ $F_{1,12} = 97.62*$ $p < 0.001$	$S = 4.48 \, Area^{0.30}$ $R^2 = 0.92$ $F_{1,12} = 138.26*$ $p < 0.001$	$S = 2.97 \, Area^{0.31}$ $R^2 = 0.67$ $F_{1,12} = 24.01*$ $p < 0.001$
Rarefied Species – Area	$RS = 7.62 \, Area^{0.07}$ $R^2 = 0.58$ $F_{1,12} = 16.40*$ $p = 0.002$	$RS = 7.60 \, Area^{0.05}$ $R^2 = 0.35$ $F_{1,12} = 6.34*$ $p = 0.028$	$RS = 5.97 \, Area^{0.11}$ $R^2 = 0.69$ $F_{1,12} = 27.17*$ $p < 0.001$	$RS = 5.15 \, Area^{0.08}$ $R^2 = 0.21$ $F_{1,12} = 3.13$ $p = 0.102$

S: bird species richness; RS: rarefied bird species richness; Area: fragment area. * significant at $\alpha = 0.05$.

Table 9. Response of rarefied bird species richness to habitat variables that varied positively with fragment area

	Spring	Summer	Fall	Winter
Rarefied bird species richness	TSD (+) $R^2 = 0.49$ $F_{1,12} = 11.76*$ $p = 0.005$	TSD (+) $R^2 = 0.40$ $F_{1,12} = 7.93*$ $p = 0.016$	TSD (+) $R^2 = 0.40$ $F_{1,12} = 7.92*$ $p = 0.016$	TSD $R^2 = 0.03$ $F_{1,12} = 0.37$ $p = 0.554$
	MTCond $R^2 = 0.05$ $F_{1,12} = 0.68$ $p = 0.425$	MTCond (+) $R^2 = 0.42$ $F_{1,12} = 8.78*$ $p = 0.012$	MTCond (+) $R^2 = 0.35$ $F_{1,12} = 6.50*$ $p = 0.026$	MTCond $R^2 = 0.10$ $F_{1,12} = 1.38$ $p = 0.263$
	OvCov (+) $R^2 = 0.49$ $F_{1,12} = 11.42*$ $p = 0.006$	OvCov $R^2 = 0.27$ $F_{1,12} = 4.34$ $p = 0.059$	OvCov (+) $R^2 = 0.30$ $F_{1,12} = 5.24*$ $p = 0.041$	OvCov $R^2 = 0.15$ $F_{1,12} = 2.14$ $p = 0.170$

TSD: tree species diversity; OvCov: overstorey cover; MTCond: mean tree condition. (+) positive relationship, indicated only for relationships that are significant at $\alpha = 0.05$.* significant at $\alpha = 0.05$.
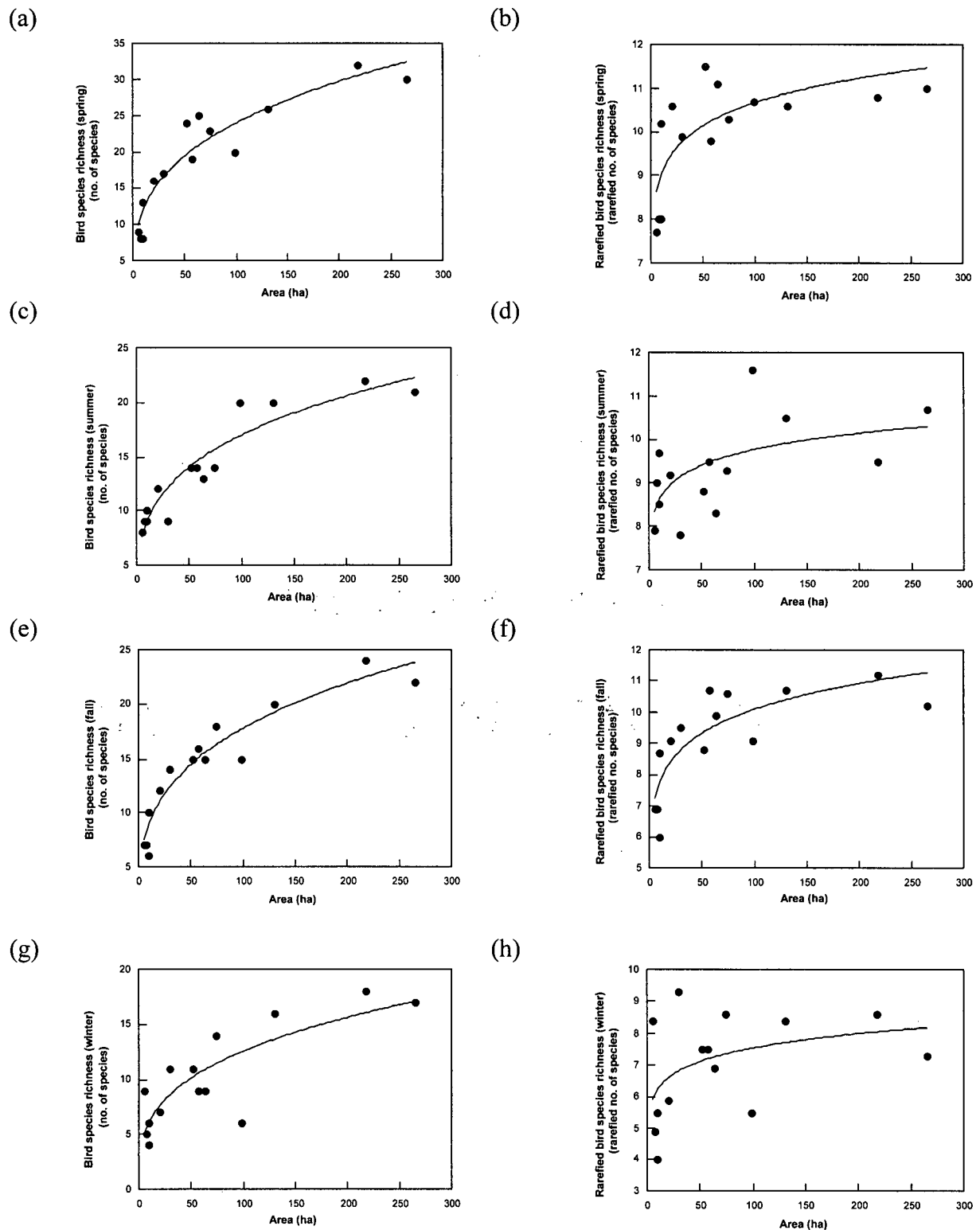
Figure 10. Bird species richness and rarefied bird species richness in relation to fragment area in (a and b) spring; (c and d) summer; (e and f) fall; (g and h) winter.

Equations for the various relationships are shown in Table 10. All relationships are significant at $\alpha = 0.05$, with the exception of the relationship between rarefied bird species richness and area in winter.

Prediction: Bird species richness in forest fragments does not respond to the diversity and/or abundance of habitat resources that remain constant with fragment area, after correcting for the effects of sampling effort

Simple linear regression of rarefied bird species richness against habitat variables that remained constant with fragment area showed that rarefied bird species richness increased significantly with tree density and total foliage cover in summer, but decreased significantly with an increase in the proportion of understorey foliage cover in winter ($p < 0.05$, Table 10).

Table 10. Response of rarefied bird species richness to habitat variables that remained constant with fragment area

	Spring	Summer	Fall	Winter
Rarefied bird species richness	Nil	TrDen (+) $R^2 = 0.42$ $F_{1,12} = 8.65*$ $p = 0.012$	Nil	UnCov (-) $R^2 = 0.45$ $F_{1,12} = 9.90*$ $P = 0.008$
		TotCov (+) $R^2 = 0.34$ $F_{1,12} = 6.09*$ $p = 0.03$		

Only habitat variables that significantly predict rarefied bird species richness are shown here ($p < 0.05$). See Appendix VIII for the non-significant fits between rarefied bird species richness and habitat variables that are constant with fragment area. Nil: no other habitat variables were significant at $\alpha = 0.05$. TrDen: tree density; UnCov: proportion of understorey foliage cover; TotCov: total foliage cover. (+) positive relationship (-) negative relationship. *significant at $\alpha = 0.05$.

Using multiple linear regression, tree density and total foliage cover were added in a forward stepwise manner to the rarefied bird species richness–tree species diversity and rarefied bird species richness–mean tree condition models for summer. Both tree density and total foliage cover added significantly to the variation explained by the models involving tree species diversity and mean tree condition respectively ($p < 0.05$, Table 11). From this, it was apparent that bird species richness would be affected by habitat variables that remained constant with fragment area, after correcting for the effects of sampling effort. This appeared to be most pronounced in summer and winter.

46

Table 11. Significant multiple regression models of rarefied bird species richness against habitat variables that varied positively and those that remained constant with fragment area in summer ($p < 0.05$)

Dependent bird variable	Independent habitat variables	
	Variable that varied positively with area	Variable that remained constant with area

Model 1: RS = 4.59 TSD + 0.01TrDen + 1.84, $R^2 = 0.63$, $F_{2,11} = 9.55$, $p = 0.004$

Rarefied bird species richness	TSD	TrDen
Cumulative R^2 and F ratio	$R^2 = 0.40$	$R^2 = 0.63$
	$F_{1,12} = 7.93*$	$F_{2,11} = 9.55*$
	$p = 0.016$	$p = 0.004$

Model 2: RS = 3.96 MTCond + 1.22 TotCov - 1.32, $R^2 = 0.64$, $F_{2,11} = 9.92$, $p = 0.003$

Rarefied bird species richness	MTCond	TotCov
Cumulative R^2 and F ratio	$R^2 = 0.42$	$R^2 = 0.64$
	$F_{1,12} = 8.78*$	$F_{2,11} = 9.92*$
	$p = 0.012$	$p = 0.003$

RS: rarefied bird species richness; TSD: tree species diversity; MTCond: mean tree condition; TrDen: tree density; TotCov: total foliage cover. *significant at $\alpha = 0.05$

Prediction: Overall bird density and density of functional bird groups in forest fragments respond positively to fragment area, and to the diversity and/or abundance of habitat resources that vary positively with area.

The response of overall bird density and density of the various functional groups to fragment area were tested using simple linear regression for each season. None of these density variables responded significantly to fragment area in winter ($p > 0.05$, Table 12). Overall bird density increased significantly with fragment area in spring, summer and fall, thereby suggesting that large fragments were supporting a higher density of birds than small fragments in those seasons ($p < 0.05$, Table 12).

Density of residents increased significantly with fragment area only in summer and fall, but migrants increased significantly with fragment area only during the spring and fall migration ($p < 0.05$, Table 12). This difference in the response of residents and migrants to fragment area may reflect differences in their use of forest fragments. Analysis of the functional bird groups revealed that only insectivore and foliage gleaner densities increased significantly with fragment

area across spring, summer and fall ($p < 0.05$), and ground gleaner density was not significantly related to fragment area in any of those seasons ($p > 0.05$, Table 12). Bark gleaner density increased significantly with fragment area only in summer and fall, and both granivore and hawker densities in spring ($p < 0.05$, Table 12).

Table 12. Response of overall bird density and density of functional bird groups to fragment area[a]

Density variable	Spring	Summer	Fall	Winter
Overall	$R^2 = 0.51$ (+) $F_{1,12} = 12.27*$ $p = 0.004$	$R^2 = 0.46$ (+) $F_{1,12} = 10.05*$ $p = 0.008$	$R^2 = 0.61$ (+) $F_{1,12} = 19.04*$ $p = 0.001$	$R^2 = 0.08$ $F_{1,12} = 1.00$ $p = 0.336$
Resident	$R^2 = 0.28$ $F_{1,12} = 4.69$ $p = 0.051$	$R^2 = 0.36$ (+) $F_{1,12} = 6.77*$ $p = 0.023$	$R^2 = 0.48$ (+) $F_{1,12} = 10.93*$ $p = 0.006$	$R^2 = 0.06$ $F_{1,12} = 0.80$ $p = 0.388$
Migrant	$R^2 = 0.46$ (+) $F_{1,12} = 10.10*$ $p = 0.008$	$R^2 = 0.03$ $F_{1,12} = 0.32$ $p = 0.582$	$R^2 = 0.37$ (+) $F_{1,12} = 6.91*$ $p = 0.022$	Insufficient data
Insectivore	$R^2 = 0.46$ (+) $F_{1,12} = 10.21*$ $p = 0.008$	$R^2 = 0.46$ (+) $F_{1,12} = 10.21*$ $p = 0.008$	$R^2 = 0.64$ (+) $F_{1,12} = 21.39*$ $p < 0.001$	$R^2 = 0.01$ $F_{1,12} = 0.11$ $p = 0.741$
Granivore	$R^2 = 0.44$ (+) $F_{1,12} = 9.55*$ $p = 0.009$	Insufficient data	Insufficient data	Insufficient data
Foliage gleaner	$R^2 = 0.34$ (+) $F_{1,12} = 6.09*$ $p = 0.030$	$R^2 = 0.39$ (+) $F_{1,12} = 7.81*$ $p = 0.016$	$R^2 = 0.50$ (+) $F_{1,12} = 11.84*$ $p = 0.005$	$R^2 < 0.01$ $F_{1,12} = 0.01^{ns}$ $p = 0.940$
Ground gleaner	$R^2 = 0.01$ $F_{1,12} = 0.09$ $p = 0.765$	$R^2 = 0.01$ $F_{1,12} = 0.06$ $p = 0.807$	$R^2 = 0.08$ $F_{1,12} = 0.98$ $p = 0.341$	$R^2 = 0.21$ $F_{1,12} = 3.11$ $p = 0.103$
Bark gleaner	$R^2 = 0.24$ $F_{1,12} = 3.74$ $p = 0.077$	$R^2 = 0.28$ (+) $F_{1,12} = 4.77*$ $p = 0.0495$	$R^2 = 0.29$ (+) $F_{1,12} = 4.85*$ $p = 0.048$	$R^2 = 0.09$ $F_{1,12} = 1.21$ $p = 0.293$
Hawker	$R^2 = 0.40$ (+) $F_{1,12} = 8.09*$ $p = 0.015$	Insufficient data	No data	No data

[a]natural logarithmic transformation applied to fragment area. Insufficient data: more than five sites without data. No data: no records in that functional group in that season. (+) positive relationship, indicated only for relationships that are significant at $\alpha = 0.05$. *Significant at $\alpha = 0.05$.

Regressing density variables against habitat variables that varied positively with fragment area (i.e. tree species diversity, mean tree condition and the proportion of overstorey foliage cover) revealed a relatively consistent pattern of covariation. With the exception of granivore density in spring, density variables that showed a significant positive response to fragment area in a particular season also showed a significant positive response to one or more of these habitat variables in the same season ($p < 0.05$, Tables 12 and 13). Tree species diversity was the most important habitat variable, with significant positive influences on overall bird density, insectivore and foliage gleaner densities in spring, summer and fall; resident density in summer and fall; and migrant density in spring and fall ($p < 0.05$, Table 13, Figure 11). To a lesser extent than tree species diversity, the proportion of overstorey foliage cover had significant positive influences on overall bird density, resident and insectivore densities in summer and fall; and on foliage gleaner density in fall ($p < 0.05$, Table 13). Bark gleaner and hawker densities increased significantly only with mean tree condition ($p < 0.05$, Table 13, Figure 12).

Table 13. Response of overall bird density and density of functional bird groups to habitat variables that varied positively with fragment area

Density variable	Spring	Summer	Fall	Winter
Overall	TSD (+) $R^2 = 0.59$ $F_{1,12} = 17.07^*$ $p = 0.001$	TSD (+) $R^2 = 0.69$ $F_{1,12} = 27.17^*$ $p < 0.001$	TSD (+) $R^2 = 0.43$ $F_{1,12} = 9.19^*$ $p = 0.011$	TSD $R^2 < 0.01$ $F_{1,12} = 0.02$ $p = 0.901$
	MTCond $R^2 = 0.09$ $F_{1,12} = 1.26$ $p = 0.284$	MTCond $R^2 = 0.22$ $F_{1,12} = 3.39$ $p = 0.091$	MTCond $R^2 = 0.18$ $F_{1,12} = 2.65$ $p = 0.129$	MTCond $R^2 = 0.10$ $F_{1,12} = 1.38$ $p = 0.264$
	OvCov $R^2 = 0.21$ $F_{1,12} = 3.14$ $p = 0.102$	OvCov (+) $R^2 = 0.33$ $F_{1,12} = 5.86^*$ $p = 0.032$	OvCov (+) $R^2 = 0.44$ $F_{1,12} = 9.53^*$ $p = 0.009$	OvCov $R^2 = 0.20$ $F_{1,12} = 3.01$ $p = 0.109$
Resident	TSD $R^2 = 0.23$ $F_{1,12} = 3.58$ $p = 0.083$	TSD (+) $R^2 = 0.38$ $F_{1,12} = 7.48^*$ $p = 0.018$	TSD (+) $R^2 = 0.32$ $F_{1,12} = 5.72^*$ $p = 0.034$	TSD $R^2 < 0.01$ $F_{1,12} = 0.04$ $p = 0.846$

Table 13. Continued.

Density variable	Spring	Summer	Fall	Winter
Resident	MTCond $R^2 < 0.01$ $F_{1,12} = 0.01$ $p = 0.944$	MTCond $R^2 = 0.16$ $F_{1,12} = 2.25$ $p = 0.159$	MTCond $R^2 = 0.20$ $F_{1,12} = 3.05$ $p = 0.107$	MTCond $R^2 = 0.10$ $F_{1,12} = 1.26$ $p = 0.283$
	OvCov $R^2 = 0.06$ $F_{1,12} = 0.77$ $p = 0.397$	OvCov (+) $R^2 = \mathbf{0.35}$ $F_{1,12} = 6.57*$ $p = 0.025$	OvCov (+) $R^2 = \mathbf{0.32}$ $F_{1,12} = 5.73*$ $p = 0.034$	OvCov $R^2 = 0.18$ $F_{1,12} = 2.57$ $p = 0.135$
Migrant	TSD (+) $R^2 = \mathbf{0.45}$ $F_{1,12} = 9.95*$ $p = 0.008$	TSD $R^2 = 0.21$ $F_{1,12} = 3.15$ $p = 0.101$	TSD (+) $R^2 = \mathbf{0.42}$ $F_{1,12} = 8.66*$ $p = 0.012$	Insufficient data
	MTCond (+) $R^2 = \mathbf{0.31}$ $F_{1,12} = 5.27*$ $p = 0.041$	MTCond $R^2 = 0.02$ $F_{1,12} = 0.20$ $p = 0.662$	MTCond $R^2 = 0.14$ $F_{1,12} = 1.99$ $p = 0.184$	
	OvCov (+) $R^2 = \mathbf{0.29}$ $F_{1,12} = 4.84*$ $p = 0.048$	OvCov $R^2 < 0.01$ $F_{1,12} < 0.01$ $p = 0.999$	OvCov (+) $R^2 = \mathbf{0.36}$ $F_{1,12} = 6.88*$ $p = 0.022$	
Insectivore	TSD (+) $R^2 = \mathbf{0.55}$ $F_{1,12} = 14.52*$ $p = 0.003$	TSD (+) $R^2 = \mathbf{0.79}$ $F_{1,12} = 43.93*$ $p < 0.001$	TSD (+) $R^2 = \mathbf{0.68}$ $F_{1,12} = 25.61*$ $p < 0.001$	TSD $R^2 < 0.01$ $F_{1,12} < 0.01$ $p = 0.948$
	MTCond $R^2 = 0.08$ $F_{1,12} = 1.08$ $p = 0.319$	MTCond $R^2 = 0.20$ $F_{1,12} = 3.09$ $p = 0.104$	MTCond $R^2 = 0.19$ $F_{1,12} = 2.73$ $p = 0.125$	MTCond $R^2 = 0.05$ $F_{1,12} = 0.67$ $p = 0.428$
	OvCov $R^2 = 0.20$ $F_{1,12} = 3.03$ $p = 0.108$	OverCov (+) $R^2 = \mathbf{0.40}$ $F_{1,12} = 8.01*$ $p = 0.015$	OverCov (+) $R^2 = \mathbf{0.50}$ $F_{1,12} = 12.17*$ $p = 0.005$	OvCov $R^2 = 0.14$ $F_{1,12} = 1.92$ $p = 0.191$
Granivore	TSD $R^2 = 0.05$ $F_{1,12} = 0.67$ $p = 0.431$	Insufficient data	Insufficient data	Insufficient data
	MTCond $R^2 = 0.10$ $F_{1,12} = 1.40$ $p = 0.259$			

Table 13. Continued.

Density variable	Spring	Summer	Fall	Winter
Granivore	OvCov $R^2 = 0.06$ $F_{1,12} = 0.75$ $p = 0.403$			
Foliage gleaner	TSD (+) $R^2 = \mathbf{0.30}$ $F_{1,12} = 5.13*$ $p = 0.043$	TSD (+) $R^2 = \mathbf{0.43}$ $F_{1,12} = 9.12*$ $p = 0.011$	TSD (+) $R^2 = \mathbf{0.49}$ $F_{1,12} = 11.71*$ $p = 0.005$	TSD $R^2 = 0.03$ $F_{1,12} = 0.34$ $p = 0.570$
	MTCond $R^2 = 0.04$ $F_{1,12} = 0.49$ $p = 0.498$	MTCond $R^2 = 0.18$ $F_{1,12} = 2.59$ $p = 0.134$	MTCond $R^2 = 0.09$ $F_{1,12} = 1.14$ $p = 0.307$	MTCond $R^2 = 0.03$ $F_{1,12} = 0.35$ $p = 0.563$
	OvCov $R^2 = 0.14$ $F_{1,12} = 1.88$ $p = 0.196$	OvCov $R^2 = 0.20$ $F_{1,12} = 3.07$ $p = 0.105$	OvCov (+) $R^2 = \mathbf{0.50}$ $F_{1,12} = 11.98*$ $p = 0.005$	OvCov $R^2 = 0.09$ $F_{1,12} = 1.17$ $p = 0.301$
Ground gleaner	TSD $R^2 = 0.01$ $F_{1,12} = 0.13$ $p = 0.725$	TSD $R^2 < 0.01$ $F_{1,12} = 0.03$ $p = 0.875$	TSD $R^2 < 0.01$ $F_{1,12} = 0.01$ $p = 0.929$	TSD $R^2 < 0.01$ $F_{1,12} = 0.01$ $p = 0.918$
	MTCond $R^2 = 0.16$ $F_{1,12} = 2.23$ $p = 0.161$	MTCond $R^2 = 0.03$ $F_{1,12} = 0.42$ $p = 0.530$	MTCond $R^2 = 0.13$ $F_{1,12} = 1.74$ $p = 0.211$	MTCond $R^2 = 0.11$ $F_{1,12} = 1.44$ $p = 0.254$
	OvCov $R^2 = 0.02$ $F_{1,12} = 0.30$ $p = 0.593$	OvCov $R^2 < 0.01$ $F_{1,12} = 0.06$ $p = 0.818$	OvCov $R^2 = 0.04$ $F_{1,12} = 0.48$ $p = 0.501$	OvCov $R^2 = 0.12$ $F_{1,12} = 1.63$ $p = 0.226$
Bark gleaner	TSD $R^2 = 0.15$ $F_{1,12} = 2.18$ $p = 0.166$	TSD $R^2 = 0.20$ $F_{1,12} = 3.06$ $p = 0.106$	TSD $R^2 = 0.16$ $F_{1,12} = 2.32$ $p = 0.154$	TSD $R^2 = 0.02$ $F_{1,12} = 0.22$ $p = 0.645$
	MTCond $R^2 = 0.26$ $F_{1,12} = 4.18$ $p = 0.063$	MTCond (+) $R^2 = \mathbf{0.32}$ $F_{1,12} = 5.60*$ $p = 0.036$	MTCond (+) $R^2 = \mathbf{0.29}$ $F_{1,12} = 4.79*$ $p = 0.049$	MTCond $R^2 = 0.05$ $F_{1,12} = 0.66$ $p = 0.432$
	OvCov $R^2 = 0.02$ $F_{1,12} = 0.20$ $p = 0.667$	OvCov $R^2 = 0.24$ $F_{1,12} = 3.78$ $p = 0.076$	OvCov $R^2 < 0.01$ $F_{1,12} < 0.01$ $p = 0.982$	OvCov $R^2 = 0.09$ $F_{1,12} = 1.23$ $p = 0.290$

Table 13. Continued.

Density variable	Spring	Summer	Fall	Winter
Hawker	TSD $R^2 = 0.15$ $F_{1,12} = 2.18$ $p = 0.119$ MTCond (+) $R^2 = \mathbf{0.45}$ $F_{1,12} = 9.85*$ $p = 0.009$ OvCov $R^2 = 0.08$ $F_{1,12} = 1.00$ $p = 0.338$	Insufficient data	No data	No data

Insufficient data: more than five sites without data. No data: no records in that functional group in that season. TSD: tree species diversity; MTCond: mean tree condition; OvCov: proportion of overstorey foliage cover. (+) positive relationship, indicated only for relationships that are significant at $\alpha = 0.05$.*Significant at $\alpha = 0.05$.
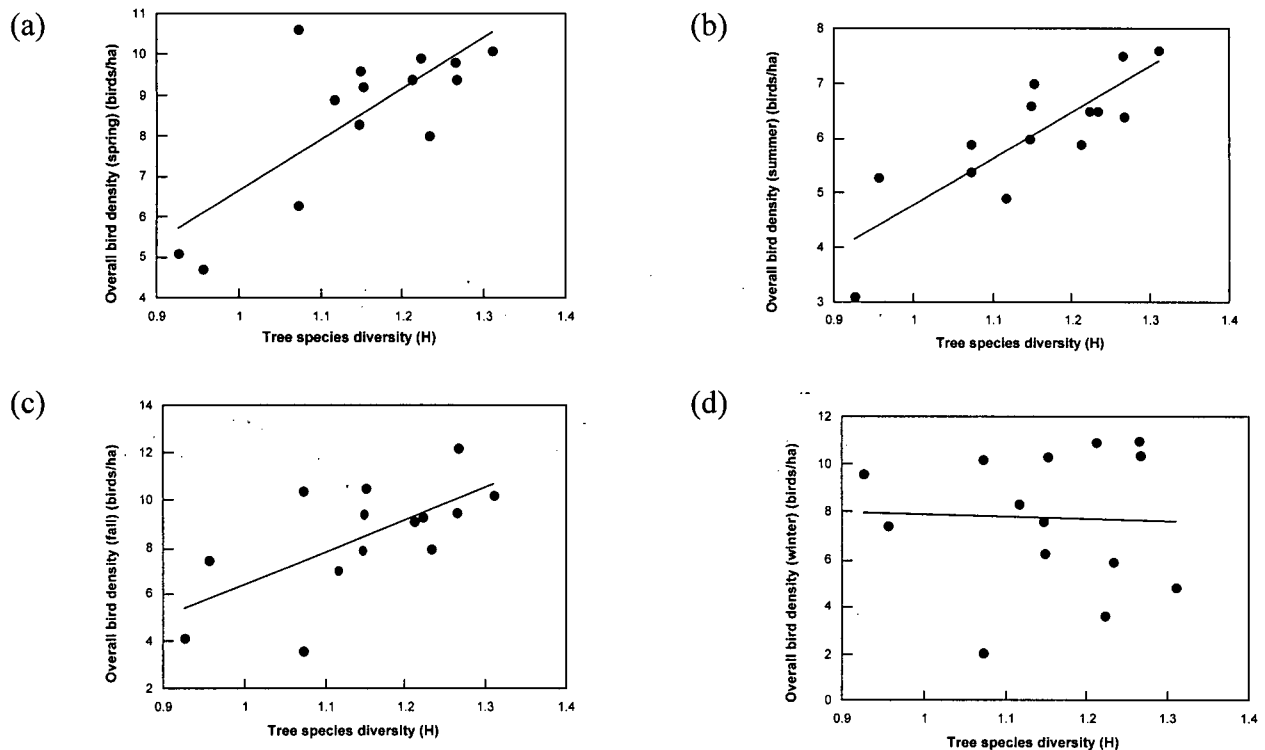
Figure 11. Relationship between overall bird density (OverallDen) and tree species diversity (TSD) in (a) spring; (b) summer; (c) fall; and (d) winter.

(a) OverallDen = 12.55TSD – 5.91, $R^2 = 0.59$, $F_{1,12} = 17.07$, $p = 0.001$; (b) OverallDen = 8.44 TSD – 3.66, $R^2 = 0.69$, $F_{1,12} = 27.17$, $p < 0.001$; (c) OverallDen = 13.82 TSD – 7.41, $R^2 = 0.43$, $F_{1,12} = 9.19$, $p = 0.011$; (d) OverallDen = 8.81 TSD – 0.93, $R^2 < 0.01$, $F_{1,12} = 0.02$, $p = 0901$.
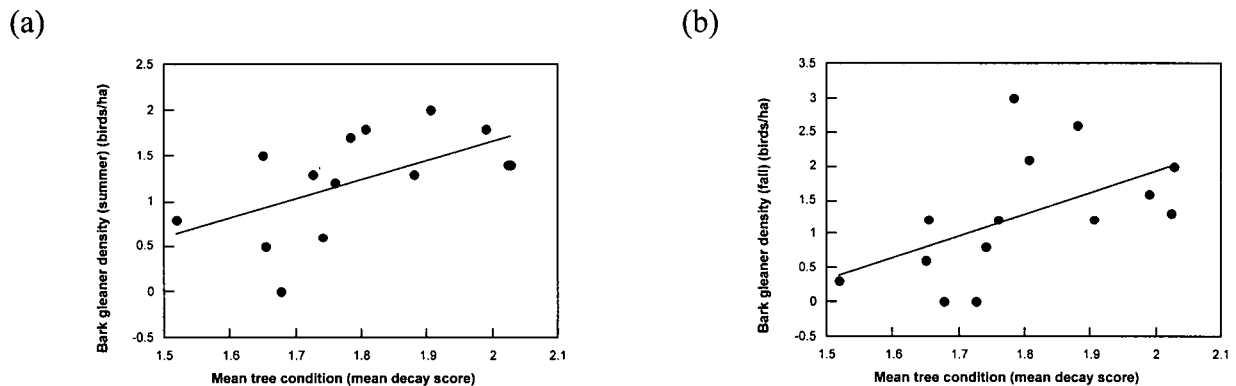
Figure 12. Relationship between bark gleaner density (BarkDen) and mean tree condition (MTCond) in (a) summer and (b) fall.

(a) BarkDen = 2.098 MTCond − 2.53, R^2 = 0.32, $F_{1,12}$ = 5.60, p = 0.036; (b) BarkDen = 3.19 MTCond − 4.46, R^2 = 0.29, $F_{1,12}$ = 4.79, p = 0.049.

Prediction: Overall bird density and density of functional bird groups in forest fragments do not respond to the diversity and/or abundance of habitat resources that remain constant with area

Simple regression analysis of overall density against habitat variables that remained constant with area showed that overall density responded negatively to the proportion of deciduous broadleaved trees and shrub density in winter (p < 0.05, Table 14, Figure 13). Hence, fragments with a high proportion of deciduous broadleaved trees that were further associated with high shrub density tended to support low densities of birds in winter. Analysis involving the density of functional bird groups also showed that resident, insectivore and foliage gleaner densities were adversely affected by the proportion of deciduous trees and shrub density in winter (p < 0.05, Table 14, Figure 13). The proportion of deciduous broadleaved trees also had a significant positive effect on migrant density and ground gleaner density in summer, while shrub density had a significant negative effect on ground gleaner density in fall (p < 0.05, Table 14). These results suggest that the effects of deciduous broadleaved trees in a predominantly coniferous forest on the bird community could be variable.

Other habitat variables that had a significant effect on the density of functional bird groups included mean tree diameter on resident density in fall; tree density on migrant density in fall and ground gleaner density in spring; total foliage cover on insectivore density in summer and migrant density in fall; proportion of understorey foliage cover on granivore density in spring and ground gleaner density in fall; foliage height diversity on foliage gleaner density in summer and fall; horizontal heterogeneity on bark gleaner density in spring, fall and winter ($p < 0.05$, Table 14). These patterns suggest that changes in the proportions of coniferous and deciduous trees would have an effect on bird community, given the association of mean tree diameter and tree density to the proportion of coniferous and deciduous broadleaved trees. They also suggest that foliage cover is a good predictor of the abundance of foraging substrates and nesting resources in these forests, and that the prevalence of numerous gaps in the forest (i.e. high horizontal heterogeneity) could have negative effects on bark gleaner density.

I further added the habitat variables described above as influential predictors of bird density in a forward stepwise manner to the significant regression models relating bird densities to habitat variables that varied positively with fragment area within the same season (i.e. tree species diversity, mean tree condition and proportion of overstorey foliage cover). Three significant multiple regression models were obtained. Mean tree diameter and tree density added significantly to the variation in resident density and migrant density respectively as explained by tree species diversity in fall, while foliage height diversity added significantly to the variation in foliage gleaner density as explained by tree species diversity in summer ($p < 0.05$, Table 15).

Overall, habitat variables that remained constant with fragment area could be important determinants of bird density. This was especially so in winter when the proportion of deciduous broadleaved trees and shrub density were found to adversely affect bird density. Habitat variables that varied positively with fragment area did not appear to be important in winter. A summary of all bird–area–habitat trends as described in this Chapter is presented in Table 16.

Table 14. Response of overall bird density and density of functional bird groups to habitat variables that remained constant with fragment area

Density variable	Spring	Summer	Fall	Winter
Overall	Nil	Nil	Nil	Conifer (+) $R^2 = 0.68$ $F_{1,12} = 26.07*$ $p < 0.001$ Decid (-) $R^2 = 0.68$ $F_{1,12} = 26.02*$ $p < 0.001$ ShDen (-) $R^2 = 0.41$ $F_{1,12} = 8.28*$ $p = 0.014$
Resident	Nil	Nil	DBH (+) $R^2 = 0.29$ $F_{1,12} = 4.93*$ $p = 0.047$	Conifer (+) $R^2 = 0.71$ $F_{1,12} = 29.11*$ $p < 0.001$ Decid (-) $R^2 = 0.71$ $F_{1,12} = 29.06*$ $p < 0.001$ ShDen (-) $R^2 = 0.43$ $F_{1,12} = 8.97*$ $p = 0.011$
Migrant	Nil	Conifer (-) $R^2 = 0.54$ $F_{1,12} = 13.88*$ $p = 0.003$ Decid (+) $R^2 = 0.53$ $F_{1,12} = 13.69*$ $p = 0.003$	TrDen (+) $R^2 = 0.35$ $F_{1,12} = 4.93*$ $p = 0.025$ TotCov (+) $R^2 = 0.28$ $F_{1,12} = 4.77*$ $p = 0.0495$	Insufficient data
Insectivore	Nil	TotCov (+) $R^2 = 0.33$ $F_{1,12} = 5.97*$ $p = 0.031$	Nil	Conifer (+) $R^2 = 0.55$ $F_{1,12} = 14.58*$ $p = 0.002$ Decid (-) $R^2 = 0.55$ $F_{1,12} = 14.41*$ $p = 0.003$

Table 14. Continued.

Density variable	Spring	Summer	Fall	Winter
Insectivore				ShDen (-) $R^2 = 0.38$ $F_{1,12} = 7.47*$ p = 0.018
Granivore	UnCov (-) $R^2 = 0.33$ $F_{1,12} = 6.04*$ p =0.030	Insufficient data	Insufficient data	Insufficient data
Foliage gleaner	Nil	FHD (+) $R^2 = 0.36$ $F_{1,12} = 6.61*$ p =0.025	FHD (+) $R^2 = 0.29$ $F_{1,12} = 4.84*$ p =0.048	Conifer (+) $R^2 = 0.71$ $F_{1,12} = 28.78*$ P < 0.001 Decid (-) $R^2 = 0.70$ $F_{1,12} = 28.57*$ p < 0.001 ShDen (-) $R^2 = 0.34$ $F_{1,12} = 6.06*$ p = 0.030
Ground gleaner	TrDen (-) $R^2 = 0.32$ $F_{1,12} = 5.65*$ p =0.035	Conifer (-) $R^2 = 0.40$ $F_{1,12} = 7.93*$ P = 0.016 Decid (+) $R^2 = 0.40$ $F_{1,12} = 7.96*$ p =0.015	ShDen (-) $R^2 = 0.50$ $F_{1,12} = 12.23*$ p = 0.004 UnCov (-) $R^2 = 0.33$ $F_{1,12} = 6.04*$ p =0.030	Nil
Bark gleaner	HH (-) $R^2 = 0.29$ $F_{1,12} = 4.84*$ p =0.048	Nil	HH (-) $R^2 = 0.44$ $F_{1,12} = 9.47*$ p =0.010	HH (-) $R^2 = 0.49$ $F_{1,12} = 11.48*$ p =0.005
Hawker	Nil	Insufficient data	No data	No data

Only habitat variables that significantly predict density are shown here (significance level $\alpha = 0.05$). See Appendix VIII for the non-significant fits between bird density and habitat variables that are constant with fragment area. Insufficient data: more than five sites without data. No data: no records in that functional group in that season. Nil: no other habitat variables were significant at $\alpha = 0.05$. Decid: proportion of deciduous broadleaved trees; DBH: mean tree diameter at breast height; TrDen: tree density; ShDen: shrub density; UnCov: proportion of understorey foliage cover; TotCov: total foliage cover; FHD: foliage height diversity; HH: horizontal heterogeneity. (+) positive relationship (-) negative relationship.*Significant at $\alpha = 0.05$.

56

(a)
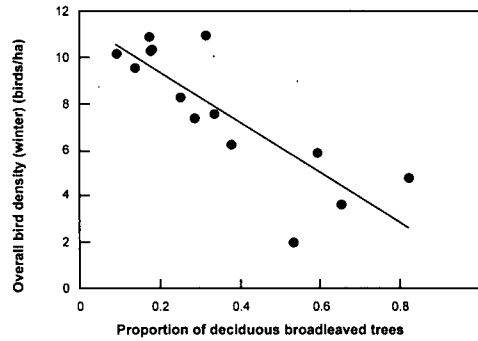
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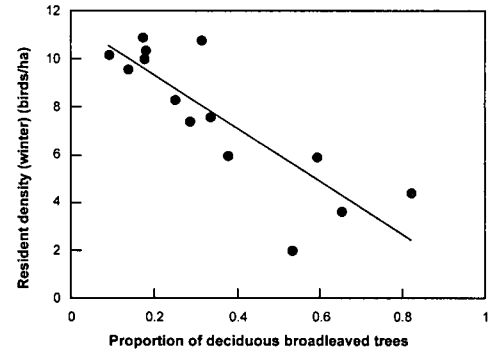
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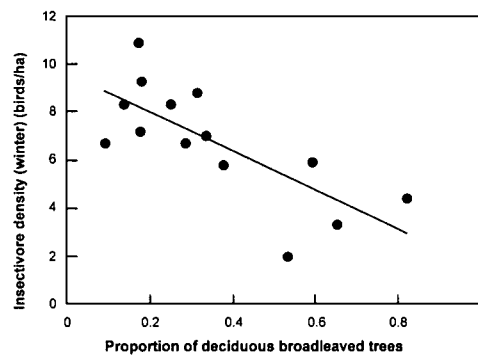
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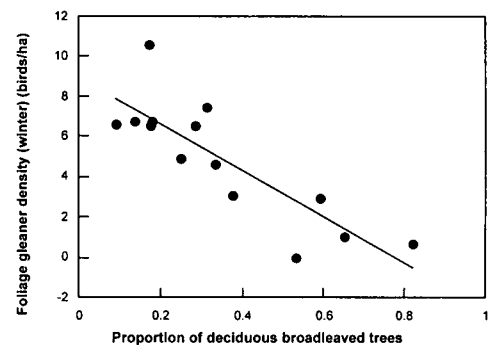
(e)
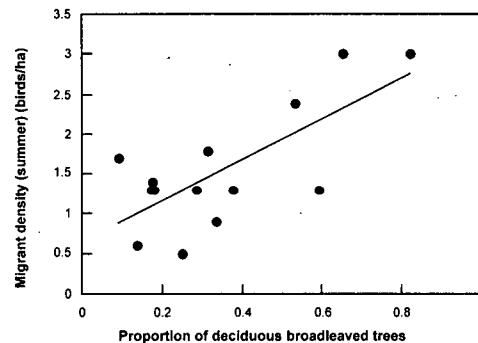
(f)
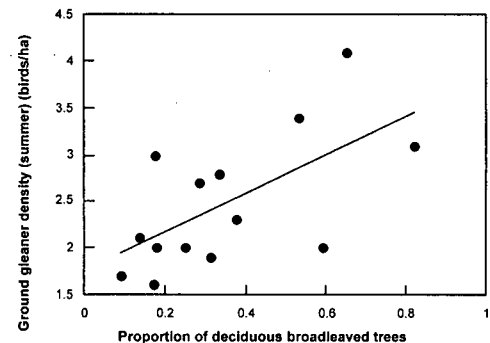
Figure 13. Relationship between bird density and proportion of broadleaved deciduous trees (Decid). (a) overall bird density (OverallDen) in winter; (b) resident density (ResDen) in winter; (c) insectivore density (InsectDen) in winter; (d) foliage gleaner density (FolDen) in winter; (e) migrant density (MigDen) in summer; (f) ground gleaner density (GdDen) in summer.

(a) OverallDen = -10.92 Decid + 11.57, R^2 = 0.68, $F_{1,12}$ = 26.02, p < 0.001; (b) ResDen = -11.14 Decid + 11.56, R^2 = 0.71, $F_{1,12}$ = 29.06, p < 0.001; (c) InsectDen = -8.088 Decid + 9.59, R^2 = 0.55, $F_{1,12}$ = 14.41, p = 0.003; (d) FolDen = -11.53 Decid + 8.91, R^2 = 0.70, $F_{1,12}$ = 28.57, p < 0.001.(e) MigDen = 2.58 Decid + 0.65, R^2 = 0.53, $F_{1,12}$ = 13.69, p = 0.003; (f) GdDen = 2.10 Decid + 1.74, R^2 = 0.40, $F_{1,12}$ = 7.96, p = 0.015.

Table 15. Significant multiple regression models of bird density against habitat variables that varied positively and those that remained constant with fragment area in fall and summer ($p < 0.05$)

Dependent bird variable	Independent habitat variables	
	Variable that varied positively with area	Variable that remained constant with area

Model 1: ResDen = 9.21 TSD + 0.18 DBH − 11.42, $R^2 = 0.57$, $F_{2,11} = 7.41*$, p = 0.009 (Fall)

Resident density	TSD	DBH
Cumulative R^2 and F ratio	$R^2 = 0.32$	$R^2 = 0.57$
	$F_{1,12} = 5.72*$	$F_{2,11} = 7.41*$
	p = 0.034	p = 0.009

Model 2: MigDen = 5.61 TSD + 0.01 TrDen - 6.61, $R^2 = 0.60$, $F_{2,11} = 8.31*$, p = 0.006 (Fall)

Migrant density	TSD	TrDen
Cumulative R^2 and F ratio	$R^2 = 0.42$	$R^2 = 0.60$
	$F_{1,12} = 8.66*$	$F_{2,11} = 8.31*$
	p = 0.012	p = 0.006

Model 3: FoliageDen = 5.34 TSD + 9.47 FHD − 19.47, $R^2 = 0.62$, $F_{2,11} = 8.91*$, p = 0.005 (Summer)

Foliage gleaner density	TSD	FHD
Cumulative R^2 and F ratio	$R^2 = 0.43$	$R^2 = 0.62$
	$F_{1,12} = 9.12*$	$F_{2,11} = 8.91*$
	p = 0.011	p = 0.005

ResDen: resident density; MigDen: migrant density; FoliageDen: foliage gleaner density; TSD: tree species diversity; TrDen: tree density; DBH: mean tree diameter at breast height; FHD: foliage height diversity.
*Significant at $\alpha = 0.05$.

Table 16. Summary of rarefied bird species richness and bird density trends in relation to fragment area and habitat variables

	Fragment Area				Habitat variables that varied positively with area												Habitat variables that remained constant with area											
					TSD				MTCond				OvCov				Conifer				Decid				DBH			
	Sp	Su	F	W	Sp	Su	F	W	Sp	Su	F	W	Sp	Su	F	W	Sp	Su	F	W	Sp	Su	F	W	Sp	Su	F	W
RS	+	+	+	.	+	+	+	.	.	+	+	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
BD	+	+	+	.	+	+	+	.	.	.	.	.	.	+	+	+	.	.	.	-	.	.	.	.	.	.	.	.
RD	.	+	+	.	.	+	+	.	.	.	.	.	.	+	+	+	.	.	.	-	.	.	+	.	.	.	+	.
MD	+	.	+	nt	+	.	+	nt	+	.	.	nt	+	.	+	nt	.	-	.	nt	.	+	.	nt	.	.	.	nt
ID	+	+	+	.	+	+	+	.	.	.	.	.	.	+	+	+	.	.	+	-	.	.	.	.	.	.	.	.
GD	+	nt	nt	nt	.	nt	nt	nt	.	nt	nt	nt	.	nt	nt	nt	.	nt	nt	nt	.	nt	nt	nt	.	nt	nt	nt
FD	+	+	+	.	+	+	+	.	.	.	.	.	.	.	+	.	.	-	+	-	.	+	.	.	.	.	.	.
GdD	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	-	.	.	.	+	.	.	.	.	.	.
BkD	.	+	+	.	.	+	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	-
HD	+	nt	nt	nt	.	nt	nt	nt	+	nt	nt	nt	.	nt	nt	nt	.	nt	nt	nt	.	nt	nt	nt	.	nt	nt	nt

Continued.

	Habitat variables that remained constant with area																											
	TrDen				ShDen				ShSD				UnCov				TotCov				FHD				HH			
	Sp	Su	F	W	Sp	Su	F	W	Sp	Su	F	W	Sp	Su	F	W	Sp	Su	F	W	Sp	Su	F	W	Sp	Su	F	W
RS	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	-	.	.	.	.	.	.	.	.
BD	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
RD	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
MD	.	.	+	nt	.	.	.	nt	.	.	.	nt	.	.	.	nt	.	.	+	nt	.	.	.	nt	.	.	.	nt
ID	.	.	.	.	.	.	.	-	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.
GD	.	nt	nt	nt	.	nt	nt	nt	.	nt	nt	nt	-	nt	nt	nt	.	nt	nt	nt	.	nt	nt	nt	.	nt	nt	nt
FD	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	+	+	.	.	+	+	.	.	.	.	.
GdD	-	.	.	.	.	.	-	.	.	.	.	.	.	.	-	.	.	.	.	.	.	.	.	.	.	.	.	.
BkD	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	-	-	-
HD	.	nt	nt	nt	.	nt	nt	nt	.	nt	nt	nt	.	nt	nt	nt	.	nt	nt	nt	.	nt	nt	nt	.	nt	nt	nt

RS: rarefied bird species richness; BD: overall bird density; RD: resident density; MD: migrant density; ID: insectivore density; GD: granivore density; FD: foliage gleaner density; GdD: ground gleaner density; BkD: bark gleaner density; HD: hawker density. Conifer: proportion of coniferous trees; Decid: proportion of deciduous broadleaved trees; TSD: tree species diversity; DBH: mean tree diameter at breast height; TrDen: tree density; MTCond: mean tree condition; ShDen: shrub density; ShSD: shrub species diversity; UnCov: proportion of understorey foliage cover; OvCov: proportion of overstorey foliage cover; TotCov: total foliage cover; FHD: foliage height diversity; HH: horizontal heterogeneity. (+): significant positive trend; (-): significant negative trend; (.): no significant trend; (nt): not tested due to insufficient or absence of data.

CHAPTER 4

DISCUSSION

LOSS IN FOREST AREA WITH URBANIZATION PREDICTS BIRD EXTIRPATIONS

The number of bird extirpations predicted from the loss of forest area in Vancouver was substantially higher than the observed number of extirpations when the prediction was based on species that were closely associated with lowland forests. A match between the predicted and observed number of extinctions was obtained only when the prediction was based on species that were closely associated with lowland forests and restricted in their geographic distribution in British Columbia. The results did not change significantly with z values of 0.20 and 0.35 (p > 0.05, Table 4). This corroborates the findings of other authors that the species–area function can give relatively accurate and robust predictions of bird extirpations with the loss in forest area, if only forest-dependent species restricted in their distribution are considered (Pimm and Askins 1995; Brooks et al. 1997; Brooks et al. 1999; Castellata et al. 2001).

Amongst the 36 bird species considered in this analysis, the three extirpated species (Spotted Owl, Yellow-billed Cuckoo and Marbled Murrelet) in Vancouver were also the most restricted in terms of their geographic distribution in British Columbia (i.e. occurrence in the least number of ecoprovinces). In particular, the former populations of the Spotted Owl and the Yellow-billed Cuckoo in Vancouver represented populations at the edge of their ranges in the Pacific Northwest (Campbell et al. 1990a; Campbell et al. 1997). The extirpation of these two species in Vancouver is consistent with the idea that populations at the edge of their ranges are sensitive to habitat loss as densities are greatest at the core and lowest at the edge (Brown 1984; Kattan et al. 1994; Christiansen and Pitter 1997). Extirpation would occur over time as these peripheral populations are negatively affected by habitat loss, unless they are rescued by

populations at the core of the range (Lawton 1993). The rescue of declining edge populations requires a healthy regional population density (Holmes and Sherry 1988; Telleria and Santos 1999). This was not the case with these two species, which had also been extirpated or experienced extensive declines in other localities across their ranges in the Pacific Northwest (Laymon and Halterman 1987; Thomas et al. 1990; DeSante and George 1994).

The mechanisms involved in the extirpation of species are usually complex. The assumption in this study is that loss of forest area is the only causal factor for the observed extirpation of species. This may not be correct. Several other potential causal factors may also contribute to the decline and extirpation of these species, in addition to forest loss. Here, I discuss two such factors. Firstly, attributes of the forest structure could be as important as the area of forest to birds. The loss in forest area in this study was defined as the conversion of forest to urban development. However, the forest in Vancouver had been logged between 1860 and 1900, prior to urbanization. The second-growth forest resulting from the logging would have lost much of the structural attributes associated with the original forest, namely large mature coniferous trees. This change in forest structure was not accounted for in the analysis. The Spotted Owl and Marbled Murrelet nest mainly in large and mature coniferous trees (Thomas et al. 1990; Ralph et al. 1995). Hence, the declines of these two species in Vancouver were likely linked not only to the loss in forest area, but also to changes in the forest structure.

Secondly, the loss of forest with urbanization is accompanied by an increase in urban habitats. The latter can bring about secondary effects on bird populations, especially through the range expansion of exotic species (e.g. European Starling) and other native species (e.g. Barred Owl) (Johnston and Garrett 1994; Root and Weckstein 1994; Marzluff 2001). These species can impact upon the viability of the original suite of native bird species through competition for nesting resources and increased predation (Wilcove 1985; Kerpez and Smith 1990). Of the three extirpated species in Vancouver, the Spotted Owl is the only species whose decline across its

range has been attributed in part to territorial competition with another species that has expanded its range, namely the Barred Owl (Dunbar et al. 1991). In Vancouver, the last published sighting of a Spotted Owl was in September 1947, whereas the Barred Owl was not recorded in Vancouver until November 1972 (Campbell 1973; Campbell et al. 1990a). It is therefore highly unlikely that the range expansion of the Barred Owl could be linked to the extirpation of the Spotted Owl in Vancouver.

Attributing time-lag in extirpation to forest loss can be difficult because of the long time interval between forest loss and eventual extirpation. Other causal factors can occur during this period and result in extirpations. Observed extirpation over time may not necessarily represent a time-lag caused by forest loss as described by Diamond (1972), Tilman et al. (1994) and Brooks et al. (1999). In addition to forest loss, the Great Blue Heron was affected by direct human exposure and disturbance, the increase in Bald Eagle (*Haliaeetus leucocephalus*) abundance and pollution off the coast of Vancouver, whereas the Band-tailed Pigeon has been overhunted (Campbell et al. 1990a, b). Hence, it may not be accurate to assume that the Great Blue Heron and Band-tailed Pigeon are likely to be extirpated with time as a result of forest loss. This may explain why the inclusion of these species as "extirpated" in the analysis did not change significantly the conclusions obtained from the initial comparisons between the observed and predicted number of extirpations (Table 4).

LARGE FOREST FRAGMENTS SUPPORT GREATER BIRD SPECIES RICHNESS AND DENSITIES THAN SMALL FRAGMENTS BECAUSE OF GREATER DIVERSITY AND/OR ABUNDANCE OF HABITAT RESOURCES

Bird responses to fragment area and habitat variables that vary positively with area

Non-linear regression fits of rarefied bird species richness against fragment area showed that large fragments supported a higher number of species in fall, spring and summer, but not in winter (Table 8). Area-dependency in breeding bird species richness has been reported by other

studies of forest fragments within urban and agricultural-urban landscapes (Lynch and Whigham 1984; Tilghman 1987a; Grover and Slater 1994; Natuhara and Imai 1999). However, the lack of area-dependency in wintering bird species richness differs from that observed by Tilghman et al. (1987b). They found that bird species richness increased significantly with area ($p < 0.05$), but did not test for the effects of sampling effort. They assumed equivalent sampling effort per unit area, although large fragments were sampled more intensively than small fragments. Hence, their observations could also be an artefact of sampling. Studies of wintering birds in forest fragments within agricultural landscapes have reported a similar lack of area-dependency in species richness to that which I observed (Yahner 1985; Hamel et al. 1993; McIntyre 1995).

The prevalence of significant positive correlations between overall bird density and area indicates a habitat resource diversity and/or abundance effect on the selection of large fragments by birds in spring, summer and fall, rather than an area *per se* effect ($p < 0.05$, Table 12) (Diamond 1970; Haila and Jarvinen 1983; Martin et al. 1995; Connor et al. 2000). Constant density across all areas in addition to a significant species–area fit is to be expected with the area *per se* hypothesis (MacArthur and Wilson 1967).

The importance of habitat resources in driving bird species–area and overall density–area patterns is reinforced by observations that significant positive correlations of rarefied bird species richness and overall density with area corresponded with similar positive correlations with tree species diversity and in some cases, also with mean tree condition and/or the proportion of overstorey foliage cover in spring, summer and fall ($p < 0.05$, Tables 8, 9, 12 and 13). All three habitat variables were positively correlated to area, suggesting that large fragments support high bird species richness and overall density because of greater tree species diversity, and/or decaying tree abundance and overstorey foliage cover. Further analysis of the densities of functional bird groups with area and these habitat variables showed that significant positive correlations between density and area corresponded with similar correlations between density

63

and one or more of these habitat variables ($p < 0.05$, Tables 12 and 13). The only exception was granivore density. Although granivore density increased significantly with area in spring ($p < 0.05$), a similar response was not found with these habitat variables. Granivore density is closely linked to seed crop abundance in the forest (Manuwal and Huff 1987; Koenig and Knops 2001). The latter is not well reflected in the habitat variables measured in this study. Nevertheless, the results corroborate previous observations of positive effects of area-dependent habitat changes on bird species richness and densities within forest fragments in urban and agricultural-urban landscapes (Lynch and Whigham 1984; Askins et al. 1987; Grover and Slater 1994).

Tree species diversity is a function of tree species richness and evenness, and was found to be positively affected by the proportion of deciduous trees ($p < 0.1$). The significant positive correlation between tree species diversity and area suggests that large fragments still maintain dominants of the mature coastal western hemlock forest (i.e. western hemlock and western redcedar), in addition to the prevalence of Douglas-fir and a deciduous broadleaved tree component ($p < 0.05$, Table 7). The importance of tree species richness in dictating bird–habitat relationships is well-documented (James and Warmer 1982; Rice et al. 1984; Hobson and Bayne 2000). More specifically, positive effects of a deciduous broadleaved tree component on breeding bird species richness and density in coniferous forests have been reported by several studies. In the Pacific Northwest, higher breeding bird species richness and density was recorded in coastal western hemlock stands with enclaves of deciduous broadleaved trees, compared to pure coniferous stands (Willson and Comet 1996). Regenerating coastal coniferous forest following clearcut logging was also found to support high breeding bird species richness and density because of a regenerating deciduous broadleaved tree component (Morrison and Meslow 1983). Potentially, the presence of a deciduous broadleaved tree component in a coniferous forest could provide supplementary foraging and nesting resources for birds, contributing to the

observed increases in rarefied bird species richness and overall density with tree species diversity in spring, summer and fall.

A high mean tree condition indicates that trees within the fragment were in later decay stages and suggests high abundance of snags, cavities and wood-boring insects (McComb and Lindenmayer 1999). The importance of these resources is reflected in the significant correlations observed between bark gleaner density and mean tree condition in summer and fall. It reaffirms current thinking about the importance of decaying standing material as a factor limiting the density of cavity nesters and bark gleaners in the forest (bark gleaners in this study are also cavity nesters) (Zarnowitz and Manuwal 1985; Martin and Eadie 1999; Weikel and Hayes 1999).

The proportion of overstorey foliage cover may be important to birds because it indicates the abundance of foraging substrates and nesting resources within the canopy. Caution is however required when interpreting the importance of overstorey foliage cover. As overstorey foliage cover increases, understorey foliage cover is expected to decrease due to light reduction. Increased overstorey foliage cover will therefore benefit overstorey birds, at the expense of understorey birds (Hansen et al. 1995; Hansen and Hounihan 1996). Hence, bird species richness and overall density should increase with overstorey foliage cover only up to a certain point.

The results are in agreement with the predictions that positive responses of bird species richness and densities to fragment area correspond with similar responses to the diversity and/or abundance of habitat resources that in turn vary positively with area. However, it is less clear whether the decline in diversity and/or abundance of these same habitat resources (i.e. tree species diversity, mean tree condition and proportion of overstorey foliage cover) can explain the lack of correlations with area for all bird variables in winter, resident and bark gleaner density in spring, migrant density in summer and ground gleaner density in all four seasons. Interpretation of these results is difficult because habitat variables were measured only in summer and changes across seasons were not tracked. Nevertheless, the lack of correlations between bird variables

and area in winter may be attributable to the drop in resources as the deciduous broadleaved trees lose their foliage. This negates the significance of large fragments with high tree species diversity to birds in winter. However, this mechanism fails to explain the observed lack of correlation between bark gleaner density and area. This is because bark gleaner density was related only to mean tree condition, which is unlikely to change in winter or in any other season. This mechanism also fails to explain the observed lack of correlations in the other seasons, as tree species diversity effects are unlikely to change substantially across spring, summer and fall.

I propose three alternative mechanisms that may explain the lack of correlations as described above. The first relates to seasonal variation in bird habitat selection. Bird habitat selection is governed by both nesting and foraging needs in summer, but more strongly governed by foraging needs in winter (Wiens 1989). Habitat selection in winter is strongly associated with the narrowing of the habitat niche (number of available foraging resource types) (Fretwell 1972). This could result in a re-distribution of bird species and abundance amongst habitat fragments on the basis of foraging resource availability, independent of area (Haila 1981; Telleria and Santos 1995). This could explain the lack of correlations with area in winter in this study. Seasonal variation in habitat selection requirements and resource availability could also explain the observed lack of correlation in resident density to habitat variables that varied positively with area in spring, relative to summer and fall (and hence lack of area-dependency in spring). In riparian vegetation in the Lower Colorado River Valley, correlations between resident bird density and habitat variables were lower in spring than in summer or fall (Rice et al. 1980, 1983; Anderson et al. 1983). They explained that high abundance of resources in spring would lower habitat selection pressures and result in low correlations between density and habitat variables. In summer, the requirements of nesting would have increased this selection pressure, although resource abundance remains relatively similar to spring. The decline in foraging resources would have commenced in fall, thereby maintaining a high habitat selection pressure despite the

66

completion of nesting. Consequently, higher correlations between density and habitat variables could be expected in summer and fall, relative to spring.

The second mechanism considers seasonal changes in bird species composition. Studies in fragmented agricultural landscapes in the southeastern United States have reported the absence of area-dependency in wintering birds and highlighted that this may be attributed to the absence of migrants within the winter bird community (Yahner 1985; Hamel et al. 1993). The bird community in my study comprised both migrant and resident species in spring and fall; had lower proportion of migrant species in summer; and was depauperate in migrant species in winter (Figure 9). The lack of correlation between rarefied bird species richness and area, and overall density and area in winter could be associated with this decline in migrant species. The decline in migrant species and shift in the composition from mainly breeders in summer to mainly transients in spring and fall may also account for differences in the response of migrant density to area.

The third mechanism considers the effects of the landscape matrix surrounding the forest fragments. Based on the present knowledge of bird habitat associations within the urban landscape matrix, several inferences of the effects of the urban landscape matrix on birds in forest fragments may be made. Firstly, insectivores are less capable of utilizing urban habitats than granivores and highly reliant on the presence of natural forest fragments within the landscape (Lancaster and Rees 1979; DeGraaf and Wentworth 1981, 1986). Secondly, ground gleaners tend to utilize urban habitats, while foliage and bark gleaners are more likely to depend on the existing forest fragments within the landscape (Lancaster and Rees 1979; Bessinger and Osborne 1982; DeGraaf and Wentworth 1981, 1986; Blair 1996). A recent study of breeding birds in Vancouver also showed that ground gleaners, such as the Spotted Towhee and Song Sparrow, were detected in greater abundance in urban areas close to forest fragments, suggesting the natal dispersal of these birds from forest fragments to the urban landscape matrix (Melles et

al. 2001). Thirdly, low food abundance in winter within forest fragments may "push" even forest-dependent bird species into the urban landscape matrix, where abundant supplementary food may be available as a result of feeding tables in residential suburbs (Jokimaki et al. 1996; Jokimaki and Suhonen 1998). These inferences agree with the observations that insectivore and foliage gleaner densities correlated significantly with area in spring, summer and fall (p < 0.05), whereas ground gleaner density did not (p > 0.05). They also explain the absence of correlations between bird variables and area in winter, underlying the importance of urban landscape matrix effects on wintering bird distribution.

Bird responses to habitat variables that remain constant with area

Contrary to the predictions, regression analysis of bird variables against habitat variables that remained constant with area showed that birds were responding to some of these habitat variables (Tables 10 and 14). In particular, mean tree diameter, tree density, total foliage cover and foliage height diversity added significantly to the variation explained by tree species diversity or mean tree condition in rarefied bird species richness, resident density, migrant density, foliage gleaner density in spring, summer and fall (p < 0.05, Tables 11 and 15). This suggests that these variables were as influential as the habitat variables that varied positively with area in these seasons. It further highlights the possibility that larger fragments may not support higher bird species richness and density, if these habitat variables are vastly altered (i.e. mean tree diameter, tree density, total foliage cover and foliage height diversity).

Three other points in relation to bird responses to habitat variables that remain constant with area can be highlighted. Firstly, the proportion of deciduous broadleaved trees had a negative effect on overall bird density and density of all functional bird groups in winter, except the ground gleaners and bark gleaners. This supports the earlier argument that rarefied bird species richness and bird densities did not respond to area in winter because of the reduced effect

of high tree species diversity, the latter arising from foliage loss in the deciduous broadleaved trees. Notwithstanding this, the proportion of deciduous trees had a positive effect on migrant and ground gleaner densities in summer. The balance between the proportions of deciduous broadleaved and coniferous trees is delicate. When the proportion of deciduous broadleaved trees increases relative to coniferous trees, a high tree species diversity will ensue and birds will benefit from this increase in resources in spring, summer and fall. Similar benefits are unlikely in winter. In fact, negative responses by the bird community would be expected due to the prevalence of deciduous broadleaved trees *per se*. This may be attributed not only to the decline in foraging resources, but to the buffering effects against the cold and wind. There is evidence that weather conditions, especially cold and wind, may influence habitat use by forest birds at northern latitudes (Grubb 1975, 1978). The prevalence of deciduous broadleaved trees is at the expense of coniferous trees, which are important shelters for birds against the cold and winds in winter (Manuwal and Huff 1987; Dellasala et al. 1996).

Secondly, habitat structure descriptors that were important could be linked to the proportions of deciduous broadleaved and coniferous trees. Mean tree diameter was positively correlated with the proportion of coniferous trees, shrub density was positively correlated with the proportion of deciduous broadleaved trees and total foliage cover was positively correlated with tree species diversity (Table 6). This highlights the concern that bird community correlations pertaining to habitat structure variables may be manifested by bird responses to floristics such as tree species composition (James and Warmer 1982; Rice et al. 1984).

Thirdly, foliage height diversity and horizontal heterogeneity may not be as important as previously thought in determining bird–habitat relationships. These habitat variables failed to significantly predict bird species richness and overall density ($p < 0.05$), unlike the findings of other authors (MacArthur and MacArthur 1962; Willson 1974; Roth 1976; Erdelen 1984). This difference may be dependent on forest type, with the effects of foliage height diversity and

horizontal heterogeneity being more apparent in open forests. Nevertheless, foliage height diversity was important to foliage gleaner density in summer and horizontal heterogeneity was important to bark gleaner density in spring, fall and winter. The importance of horizontal heterogeneity may not be related to the diversity of foraging resources across a horizontal spatial plane. It could be related to the openness of the forest. Support for this could be seen from the significant negative correlations between bark gleaner density and horizontal heterogeneity ($p < 0.05$). High horizontal heterogeneity would arise from the large number of gaps interspersing the forest canopy. This may be less attractive to bark gleaners such as the Brown Creeper, which tends to avoid gaps when foraging (Weikel and Hayes 1999).

The relationship between bird species richness and density, and area were driven to a certain extent by habitat variables that varied positively with area. However, the mechanism driving bird species–area and bird density–area patterns is not straightforward. Other mechanisms related to seasonal variation in bird habitat selection, seasonal changes in bird species composition and urban landscape matrix effects are possibly operating in tandem with the diversity and/or abundance of habitat resources that varied positively with area. It is important to recognize that birds were also responding to habitat variables independent of area. Most of these variables may be linked back to the relative proportions of deciduous broadleaved and coniferous trees in the fragments.

Limitations

This study to test the hypothesis that large fragments can support more bird species and density than small fragments due to greater diversity and/or abundance of habitat resources has several limitations. Firstly, bird density was used as the response variable to habitat variables. In doing so, I assumed that density is a direct measure of the quality of habitat. This can be misleading because density does not always relate to the survivorship and fecundity of species

(van Horne 1983; Vickery et al. 1992). The results of this study should ideally be complemented by demographic studies of indicator bird species (Easton and Martin 1998; Marzluff 2001). In addition, the measurement of density may be confounded by seasonal changes in bird behaviour. For example, the flocking of birds in winter can increase the probability of detection and affect estimates of winter densities. Corrections for flocking can be done by weighted linear regression of flock size on distance, as recommended by Buckland et al. (1993). However, a large sample size and accurate distances to all observations are required, making corrections difficult. Density in fall could also have been underestimated because several migrant species had departed from the study area prior to the commencement of the fall survey in September (only 8 migrant species were detected in fall, compared to 17 migrant species in spring). This was inevitable because August is the transition period between breeding and fall migration. It would have been difficult to distinguish individuals of these species that were breeding in the forest fragments from those that were transiting southwards, if surveys were conducted throughout August. Nevertheless, the seasonal trend in bird density obtained in this study was consistent with that reported by Lancaster and Rees (1979) from transect counts in a forest fragment within Pacific Spirit Regional Park.

Secondly, the use of habitat variables to approximate the diversity and/or abundance of habitat resources is in itself an assumption. It further assumes that birds cue on habitat features that are in turn correlated to food abundance (Wiens 1989). Very few studies have actually measured the abundance of food or nesting resources because of the logistical difficulties involved (Robinson 1998).

Last but not least, this study was conducted over a single year. Bird habitat relationships derived from a single year study may be misleading due to between-year density variation within the same study plot (Wiens 1981). Such variation can arise from the vagaries of weather or from

other factors affecting the population dynamics of birds. An additional year of replication would have been preferable to detect variation brought about weather conditions.

IMPLICATIONS FOR LAND-USE PLANNING AND MANAGEMENT OF FOREST FRAGMENTS IN URBAN LANDSCAPES

Results from this study have important urban land-use planning and management implications, given the premise that society values having the full natural complement of species in ecosystems (referred to throughout this thesis as "maximization of species diversity"). The hypothesis that the loss in forest area in the landscape with urbanization results in bird extirpations as expressed by the species–area function cannot be rejected in the light of the results obtained from this study. Bird species closely associated with lowland forests and restricted in their geographic distribution in British Columbia are most prone to extirpation. Habitat loss with urbanization is a likely cause of extirpation in some bird species. Other causes such as changes in forest structure, expansion of exotic and other native species may compound the effects of habitat loss and exacerbate the number of extirpations. This result has important implications on the current urban land-use planning paradigm.

Conventional urban land-use allocation is dictated by economic (e.g. business districts and industry) and social (e.g. residential districts) interests at the onset of urban development. Natural habitat conservation is rarely accorded any priority at this stage and is restricted to residual areas of little or no development value. The desire to incorporate the conservation of habitat fragments with natural attributes into urban land-use plans is often realized only years after initial plans have been drawn up and implemented. The initial loss of habitats would have already resulted in extirpations, thereby greatly reducing the conservation value of any of the remaining habitat. A land-use planning paradigm such as this results not only in the extensive reduction of natural habitats within cities, but is the precursor to urban sprawl. A response to this in recent years has been the development of the compact city concept where land-use within the

72

existing city is intensified and green open space around the city is retained (Hidding and Teunissen 2002). The current urban growth management legislation in Oregon and Washington, and the "green zone" concept in Vancouver are examples of the compact city concept (GVRD 1993; Ferguson et al. 2001). This concept places new threats to the already small amounts of natural habitats present in cities, upon which the persistence of wildlife species already vulnerable to extirpation is dependent. For example, the Western Screech-Owl was identified as one of the species likely to become extirpated in this study. Although not extirpated yet, it is declining in Vancouver as a result of continual loss of lowland coniferous forest, as well as possible competition from Barred Owls (Dr Jamie Smith and Kyle Elliot pers. com., 2 and 21 May 2002). A shift in the land-use planning paradigm from one based solely on social and economic factors to one that places importance on the incorporation of natural habitats from the onset is needed, if we are to achieve the urban wildlife management goal of maximizing species diversity within the landscape.

Shifting from the landscape level to the forest fragment level, I tested the hypothesis that the fragmentation of the remaining forest into fragments with urbanization results in large fragments having greater bird species richness and densities than small fragments because of greater diversity and/or abundance of habitat resources. The results showed that large fragments supported higher bird species richness and density than small fragments, at least in spring, summer and fall. This may be attributed especially to greater tree species diversity and abundance of decaying standing material (i.e. greater mean tree condition) in large fragments. From a management perspective, this highlights the importance of retaining as much of the larger fragments as possible in order to achieve the goal of maximizing within-patch species diversity, as advocated by other urban ecologists (Murphy 1988; Raedeke and Raedeke 1995; Juricic and Jokimaki 2001; Marzluff and Ewing 2001). More importantly, retention of large fragments alone is not enough. There must be a concerted effort to ensure that these fragments

73

continue to maintain the high diversity and/or abundance of habitat resources that make them attractive to birds in the first instance, e.g. maintenance of high tree species diversity and retention of decaying standing material.

This study also showed that birds will respond to habitat resources that remain constant with area. Of importance is the proportion of deciduous broadleaved trees in the forest fragments, which may be directly or indirectly (as a component of tree species diversity) important to birds in spring, summer and fall, but have adverse effects in winter (Table 17). In the context of Vancouver, this result addresses the issue of whether deciduous broadleaved trees in forest fragments should be removed in favour of coniferous trees. Proponents of this would argue that their removal would help to restore the forest to its original condition. Opponents argue that the deciduous broadleaved trees provide important supplementary food source to wildlife. The results suggest that if the deciduous broadleaved tree component was allowed to proliferate, it could have detrimental effects on birds in winter. Even though deciduous broadleaved trees may have been shown to have a direct or indirect positive effect on bird species richness and density in the other seasons, a threshold probably exists. Where too much of the coniferous tree component is replaced by deciduous broadleaved trees, one can expect major changes in the bird species composition, possibly with more ground gleaners and fewer bark gleaners (Holmes and Sherry 2001). At the same time, any restoration effort involving the replacement of the deciduous broadleaved tree species with coniferous tree species must be monitored over time. There is no guarantee that the forest ecosystem would respond to such restoration according to the usual trends of succession because many of these forest fragments have been vastly altered (Hobbs 1988; Agee 1995). Perhaps, one should adopt the management approach of "benign neglect" as suggested by Niemela (1999). This approach involves management prescriptions that include leaving certain areas unmanaged, some areas lightly managed and others intensively managed. Much would depend on the site conditions and

characteristics. To this, I would add the need to practise adaptive management so that the effects of management prescriptions are continually monitored and modified to achieve the desired goals (Holling and Meffe 1995).

Table 17.   General effects of deciduous broadleaved trees on birds in forest fragments in Vancouver

Relative proportions of deciduous broadleaved trees and coniferous trees	Tree species diversity	Overall bird density	
		Breeding season	Non–breeding season
Deciduous broadleaved trees: Low Coniferous trees: High	Low	Low	High
Deciduous broadleaved trees: Moderate Coniferous trees: Moderate	High	High	Moderate
Deciduous broadleaved trees: High Coniferous trees: Low	Low	Moderate	Low

CHAPTER 5

CONCLUSION

Habitat modification with urbanization encompasses two processes – habitat loss and fragmentation. In this study, I investigated the effects of these two processes on forest bird communities in Vancouver, British Columbia. I tested the hypotheses that (1) the loss in forest area in the landscape with urbanization results in bird extirpations as expressed by the species–area function; and (2) the fragmentation of the remaining forest with urbanization results in large fragments having greater bird species richness and densities than small fragments because large fragments contain a greater diversity and/or abundance of habitat resources.

I validated the first hypothesis by testing the prediction that the observed number of bird extirpations due to the loss in forest area would match that predicted by the species–area function. By estimating the area of forest loss in Vancouver since 1859 and reviewing the conservation status of birds in Vancouver, I showed that this prediction was correct with bird species closely associated with lowland forests and restricted in their geographic distribution in British Columbia. This result did not change significantly with the inclusion of species considered as likely to become extirpated with time. Notwithstanding these results, the mechanisms resulting in species extirpations are complex. Other possible causal factors, including changes in forest structure and the expansion of introduced and native species, must also be considered together with forest loss.

I proceeded to validate the second hypothesis by testing the predictions that bird species richness and densities would respond positively to fragment area and to habitat variables that varied positively with area, but would not respond to habitat variables that remained constant with area. Using bird and habitat data collected in 14 forest fragments in Vancouver and lower

76

West Vancouver, I showed that where bird species richness, overall density and density of functional bird groups responded positively to fragment area, these responses could be related to the positive covariation of area and habitat variables, especially tree species diversity and mean tree condition (approximates the abundance of decaying standing material). However, failure of this mechanism to fully explain the lack of correlation between the density of some functional bird groups and area across the seasons suggests that other mechanisms may be acting in tandem. These mechanisms may include seasonal variation in bird habitat selection, seasonal changes in bird species composition and urban landscape matrix effects. The results also showed that bird species richness and density were responding significantly to habitat variables that remained constant with area, opposite to the predictions. This suggests that there is a possibility that birds may not even select for large fragments despite the greater diversity and/or abundance of habitat resources, if resources that are independent of area are changed dramatically. Overall, the results provide some support for the hypothesis that large fragments have greater bird species richness and densities than small fragments because of greater diversity and/or abundance of habitat resources. At the same time, the complexity of bird–area–habitat relationships is highlighted.

In line with the urban wildlife management goal of maximizing species diversity at the landscape and within-patch scales, the results of this study imply that there is a need to consider (1) the incorporation of nature conservation into urban land-use plans from the onset; (2) the retention of large fragments must be done together with the identification and maintenance of habitat characteristics that supply fragments with critical resource requirements for birds.

Future studies should further validate the results obtained from this study by focussing on population demographic factors. There is also an urgent need to separate the effects of within-patch and landscape matrix effects on bird communities within forest fragments.

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81

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APPENDIX I

WEATHER DATA

Figure A. Normal mean daily temperature (circles) and total precipitation (squares) in Vancouver, from the Vancouver International Airport weather station (49°11' N, 123°11' W) between 1937–1990. Source: Meteorological Service of Canada (2002).
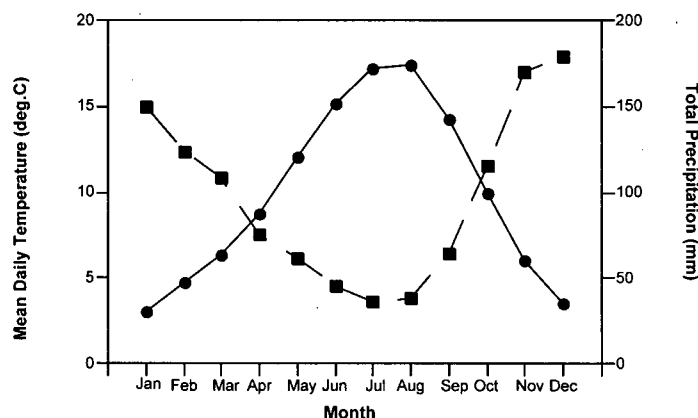
Figure B. Comparison of (a) mean daily temperature (circles) and (b) total monthly precipitation (circles) for the study period (April 2001 to January 2002) against the normal mean daily temperature and total monthly precipitation (squares) (1937 to 1990). Records are from the Vancouver International Airport weather station (49°11' N, 123°11' W). Source: Meteorological Service of Canada (2002).
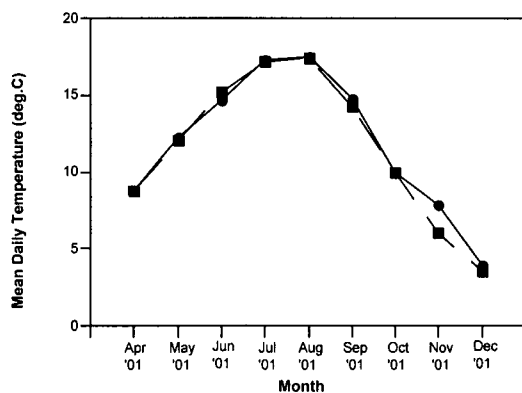
(a)   (b)
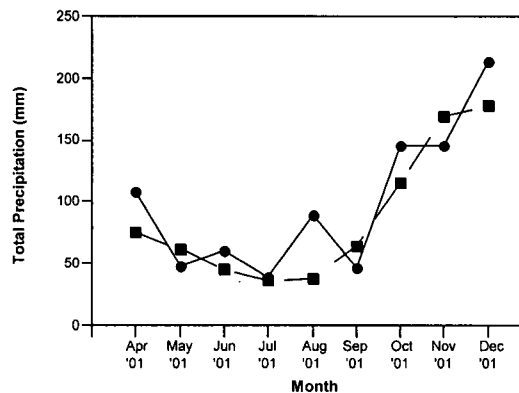
APPENDIX II

LOCATION OF TRANSECTS

Site	Transect No.	Direction of traverse from start to end of transect	UTM reference for the start of transect	UTM reference for the end of transect
Brockton 49°18'03''N, 123°07'38''W	T1	90°	490625E 5460950N	490825E 5460950N
Campus-S 49°15'08''N, 123°14'35''W	T1	67.5°	482200E 5455500N	482375E 5455575N
16th-Uni Blvd-N 49°15'44''N, 123°14'00''W	T1	135°	482850E 5456875N	483975E 545725N
Musqueam 49°13'57''N, 123°11'40''W	T1	157.5°	485800E 5453125N	485875E 5452975N
Shaughnessy 49°14'20''N, 123°12'40''W	T1	112.5°	484400E 5453775N	484625E 5453725N
	T2		484775E 5453625N	484950E 5453550N
W-Park Dr 49°18'26''N, 123°09'10''W	T1	202.5°	489100E 5462125N	489025E 5461950N
	T2		488800E 5461750N	488725E 5461550N
16th-Uni Blvd-S 49°15'34''N, 123°13'28''W	T1	270°	484250E 5456325N	484050E 5456325N
	T2		483950E 5456450N	483750E 5456450N
	T3		483400E 5456500N	483200E 5456500N
Uni-Chancellor Blvd 49°16'11''N, 123°14'00''W	T1	225°	483450E 5457400N	483325E 5457250N
	T2		483275E 5457500N	483150E 5457350N
	T3		483050E 5457600N	482925E 5457450N

Continued.

Site	Transect No.	Direction of traverse from start to end of transect	UTM reference for the start of transect	UTM reference for the end of transect
E-Causeway 49°18'21''N, 123°08'28''W	T1	180°	489875E 5461800N	489875E 5461600N
	T2		489675E 5461525N	489675E 5461325N
	T3		489750E 5461050N	489750E 5460850N
Lighthouse 49°20'06''N, 123°15'40''W	T1	180°	480650E 5464675N	480650E 5464475N
	T2		481050E 5464825N	481050E 5464625N
	T3		481300E 5464775N	481300E 5464575N
N-Chancellor Blvd 49°16'29''N, 123°14'00''W	T1	180°	482450E 5458400N	482450E 5458200N
	T2		482825E 5458375N	482825E 5458175N
	T3		483375E 5458300N	483375E 5458100N
W-Causeway 49°18'15''N, 123°09'00''W	T1	0°	488675E 5460675N	488675E 5460875N
	T2		489275E 5460700N	489275E 5460900N
	T4		489150E 5461075N	489150E 5461275N
	T5		489175E 5461550N	489375E 5461550N
S-16th Ave 49°14'45''N, 123°13'00''W	T1	90°	483400E 5456000N	483600E 5456000N
	T2		483850E 5455875N	484050E 5455875N
	T3		485000E 5455900N	485200E 5455900N
	T4		483525E 5455350N	483725E 5455350N
	T5		484100E 5455700N	484300E 5455700N
	T6		484450E 5455500N	484650E 5455500N

Continued.

Site	Transect No.	Direction of traverse from start to end of transect	UTM reference for the start of transect	UTM reference for the end of transect
N-SW Marine 49°15'15''N, 123°13'00''W	T1	135°	484250E 5454350N	484400E 5454225N
	T2		484900E 5454025N	485050E 5453875N
	T3		485550E 5453925N	485675E 5453800N
	T4		485450E 5454425N	485575E 5454275N
	T5		484675E 5454500N	484400E 5454350N
	T6		483600E 5454825N	483775E 5454750N
	T7		483650E 5454500N	483775E 5454350N

APPENDIX III

PRELIMINARY STUDY

INTRODUCTION

A preliminary survey was conducted prior to the study. The aims of this preliminary survey were: (1) to determine the optimal observer rate of movement or the census duration when using a line transect[5]; (2) to determine the total length of transect required to achieve a given coefficient of variation and hence, determine the number of transects in each study site (or forest fragment). Both the rate of observer movement and the total length of transect used have been shown to have an effect on the precision of the estimates of bird abundance (Er et al. 1995; Harden et al. 1986; Krebs 1989; Buckland et al. 1993). This preliminary survey was conducted in three forest fragments that were eventually also used as sites in the main study. They were S-16th Ave (49°14'45''N, 123°13'00''W), N-SW Marine (49°15'15''N and 123°13'00''W) and W-Causeway (49°14'45''N and 123°13'00''W).

EXPERIMENTAL DESIGN

Six transects, each 200 m long, were randomly located within each study site. A common direction (to the nearest 22.5 degrees) was randomly selected for transects within each site. The transects were at least 200 m apart and were at least 50 m from the edge of the site. They did not cross any forest trails. The centre lines of the transects were marked at 5 m intervals with red flagging tape.

I applied three census durations to the 200 m-long transects – 12 min, 18 min and 24 min. This translated to a movement rate of 1 km/h (similar to Bibby et al. 2000), 0.67 km/h (similar to

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[5] Results pertaining to this part of the study has been accepted for publication: Er, K.B.H., J.L. Innes and A.Kozak. 2002. Effects of census duration on estimates of winter bird abundance and species richness along line transects in coastal coniferous forest fragments. Journal of Field Ornithology 73: in press.

Harden et al. 1986, Wiebe and Martin 1998, and approximating to that of Ralph et al. 1993, De Santo and Willson 2001) and 0.5 km/h (similar to Holmes and Sturges 1975, Harden et al. 1986). To control for temporal changes in bird activity and variation across study sites, the transects were blocked across three fortnights and the three study sites in a replicated Latin Square design (i.e. 2 squares x 3 study sites x 3 fortnights) (Neter et al. 1996; Merrill et al. 2000) (Figure A). Census durations were randomly assigned to each transect in the manner recommended by Neter et al. (1996). Each transect was surveyed twice with the assigned census duration within the pre-determined fortnight. The order in which the transects were surveyed within each fortnight was randomized. Surveys were confined to the first two hours after sunrise and days without rain or strong wind. A single observer (K. Er) conducted the surveys over six weeks in winter, from 7 January to 3 February 2001. The survey protocol was similar to that used in the study proper (described in detail in Chapter 2). All individual birds were recorded within 50 m of each transect. The mean number of individual birds and number of bird species detected in each transect were obtained from the two surveys.

This experimental design ensured that observations were independent, as census durations were applied randomly to different transects in each study site for each fortnight. This differs from a design where the census durations are tested on the same transects such that observations are not independent and not amenable to parametric statistical testing. This design was also unique in that the row and column blocks were the same from square to square (i.e. same fortnights and study sites for the two squares), and not nested within squares as in a usual Latin Square. This design can be expressed as follows:

$$Y_{ijkh} = \mu + \rho_h + \tau_j + \alpha_i + \beta_k + (\rho\tau)_{hj} + (\rho\alpha)_{hi} + (\rho\beta)_{hk} + \varepsilon_{ijk(h)}$$

where Y_{ijkh} is the observation of treatment j in row i and column k of the square h, ρ_h is the effect of the square or replication, τ_j is the treatment (i.e. census duration) effect, α_i is the row (i.e. fortnight) effect, β_k is the column (i.e. study site) effect, $(\rho\tau)_{hj}$, is the interaction effect between

the squares and treatments, $(\rho\alpha)_{hi}$ is the interaction effect between the squares and rows, $(\rho\beta)_{hk}$ is the interaction effect between the squares and columns, and $\varepsilon_{ijk(h)}$ is the experimental error effect.

SQUARE 1

FORTNIGHT	STUDY SITES		
	N-SW Marine	S-16th Ave	W-Causeway
Fortnight 1 (7-20 Jan 01)	A/T5	C/T1	B/T1
Fortnight 2 (21 Jan-3 Feb 01)	C/T3	B/T6	A/T5
Fortnight 3 (4-17 Feb 01)	B/T1	A/T3	C/T3

SQUARE 2

FORTNIGHT	STUDY SITES		
	N-SW Marine	S-16th Ave	W-Causeway
Fortnight 1 (7-20 Jan 01)	B/T4	A/T4	C/T2
Fortnight 2 (21 Jan-3 Feb 01)	A/T6	C/T5	B/T4
Fortnight 3 (4-17 Feb 01)	C/T2	B/T2	A/T6

Figure A.   Latin Square design for the study.

Treatments of census duration - A: 12 minutes (1 km/h movement rate); B: 18 minutes (0.67 km/h movement rate); C: 24 minutes (0.5 km/h movement rate). T1 to T6 denotes transects in respective study sites. Each transect was surveyed twice within the respective fortnight.

DATA ANALYSIS AND RESULTS

Determination of rate of movement or survey duration along transect

The Latin Square model was fitted to each of the dependent variables. Analysis of variance was used to test the null hypotheses that variation in census duration would not bring about significant changes to the number of individual birds and bird species detected. A natural logarithmic transformation was applied to the number of individual birds to ensure normality. Where significant changes were obtained, Bonferroni's multiple comparison test was used to compare the number of individual birds and bird species detected with different census durations.

A total of 482 individual birds, comprising 25 species, were detected in this study. Census duration significantly affected the number of individual birds and the number of species detected ($p < 0.05$, Table A). In all the models, the statistical effects of squares, fortnight and study site, as well as the interaction terms, were not significant ($p > 0.05$, Table A). Hence, variation across fortnights and study sites did not confound the effects of census duration in these models. The number of individual birds detected increased significantly with the increase in census duration from 12–18 min, but not from 18–24 min ($p < 0.05$). The number of bird species detected also increased with census duration. However, the number of bird species detected did not increase significantly from 12–18 min, or from 18–24 min ($p < 0.05$). A significant difference was found only between 12 min and 24 min ($p < 0.05$, Table B).

Table A.   Analysis of variance of the number of individual birds and number of bird species.

Variables	DF	Number of individual birds[a]		Number of bird species	
		$F_{2,4}$	P-value	$F_{2,4}$	P-value
Census Duration	2	30.02	0.004	10.40	0.026
Study Site	2	2.27	0.220	0.20	0.826
Fortnight	2	3.26	0.144	0.45	0.666
Square	1	0.36	0.579	2.40	0.196
Square*Census Duration	2	4.00	0.111	3.20	0.148
Square*Study Site	2	1.03	0.437	1.40	0.346
Square*Fortnight	2	2.56	0.192	2.15	0.232
Error	4	-	-	-	-

[a]Natural logarithmic transformation has been applied to the number of individual birds.

Table B.   Comparison of the number of individual birds and number of bird species detected across different census durations[1].

Census duration (mins)	Number of individual birds (birds/transect)	Number of bird species
12	1.9[a] (6.4)	4.2[a]
18	2.7[b] (14.7)	5.8[ab]
24	2.8[b] (17.2)	6.5[b]

[1]Data presented refer to mean values. For the number of individual birds, the mean values without brackets are in the natural logarithmic scale and those in brackets are the "back-transformed" means. [ab]Means with the same letter are not significantly different (significance level, $P < 0.05$) (based on Bonferroni's multiple comparison test).

99

From these results, it seems that a census duration of 18 min is most efficient for detecting bird abundance (i.e. the number of birds). Although a greater census duration would result in the detection of more bird species, this is unlikely to be significant. Any further increase in census duration would also bring about greater observer exposure to the birds. This can bring about the potentially more serious problem of not recording the birds at their initial location prior to movement in response to the observer and can increase the tendency of double counts. Consequently, estimates of bird abundance would be biased. For these reasons, a census duration of 18 mins for a 200 m-long transect was adopted for the main study.

Determination of the total length of transect and the number of transects

I used the preliminary results from the largest site (N-SW Marine) to calculate the total length of transect required to survey that particular site for three given coefficients of variation (10%, 15% and 20%). I used data for bird numbers pooled from transects that had been surveyed with a census duration of 18 mins for this calculation. This was as follows:

$$L = \left(\frac{3}{CV^2}\right) x \left(\frac{L_0}{N_0}\right) ,$$

where L is the total length of transect required (km), CV is the desired coefficient of variation, L_0 is the length of the transect in the preliminary survey (0.4 km) and N_0 is the mean number of birds obtained from the survey of the 0.4 km-transect (39 birds) (Krebs 1989).

For a CV of 10%, the length of transect required was approximately 3.1 km. This worked out to approximately 15 200m-long transects. For a CV of 15%, the length of transect decreased to approximately 1.4 km or seven 200m-long transects. This decreased further to approximately 0.8 km or approximately four 200m-long transects for a CV of 20% (Table C). Krebs (1989) highlighted the need to balance between statistical soundness and logistical constraints. Whilst a CV of 10% would have been desirable, it was not possible to place 15 200m-long transects

within the site because of the presence of recreational trails. The placement of seven 200m-long

transects was possible and I decided on this at the expense of 5% of coefficient of variation.

Table C. Total length of transects corresponding to various desired coefficient of variation (CV).

Desired CV	Total length of transects (km)	No. of 200m-long transects
10%	3.1	15
15%	1.4	7
20%	0.8	4

Buckland et al. (1993) provided a guideline to decide if the length of the transect was

adequate. As a practical minimum, they recommended that the length of the transect should

allow for the detection of at least 60–80 birds or any other "objects" of interest. To test if the

calculated length based on a CV of 15% was appropriate, I calculated the number of birds that

would have been detected if the proposed length of 1.4 km was used. This is as follows:

$$L_0/N_0 = L/N \Rightarrow N = N_0/L_0 \times L \text{ ,}$$

where L_0 is the total length of the transect used in the preliminary survey (0.4 km), N_0 is the

mean number of birds obtained from the survey of the 0.4 km-transect (39 birds), L is the total

length of transect proposed and N is the expected number of birds that would be obtained from

the survey of the proposed total length of transect.

For a total transect length of approximately 1.4 km, I calculated that this would yield

approximately 133 birds. This is greater than the minimum guideline provided by Buckland et al.

(1993). I therefore concluded that the use of a coefficient of variation of 15% was still

acceptable, and that the use of a total transect length of 1.4 km or approximately seven 200 m-

long transects would still give reasonably precise estimates of bird abundance.

From here, I then allocated the number of 200 m-long transects that should be placed in the

study sites or fragments by using the allocation of seven transects to the largest site (N-SW

Marine) as a base. This was done by first allocating the number of transects according to fixed size classes ranging from 0–300 ha. This range was used because all the study sites fell within this size range. The number of transects to be placed in each study site corresponded to the number allocated to the size class. This is as shown in Table D.

This preliminary survey was conducted during the non-breeding season in winter. Due to the constraint of time, I was unable to test the results here in the breeding season. However, if one assumes that birds are less vocal during the non-breeding season (Best 1981) and therefore are less likely to be detected, then the results here would reflect a "worst-case" scenario. The sampling protocol developed on the basis of the results of this survey in the study proper would by the same reasoning be more than adequate to deal with variation within the breeding season.

Table D. Allocation of the number of 200m-long transects in each of the fragments selected as study sites in the study proper.

Study sites	Size class (ha)[b]	Area (ha)	Number of bird survey transects
Brockton	0-10	5.6	1
Campus-S	0-10	7.8	1
16th-Uni Blvd-N	0-10	9.1	1
Musqueam	0-10	9.7	1
Shaughnessy	10-50	20.1	2
W-Park Dr	10-50	30.0	2
16th-Uni Blvd-S	50-100	51.5	3
Uni-Chancellor Blvd	50-100	56.7	3
E-Causeway	50-100	63.6	3
Lighthouse	50-100	73.5	3
N-Chancellor Blvd[a]	50-100	98.7	3
W-Causeway	100-150	130.2	4
S-16th Ave	200-250	217.9	6
N-SW Marine	250-300	265.2	7

[a] When estimating the area of N-Chancellor Blvd, I excluded areas of major ravines, which were inaccessible in this instance and impossible to survey.
[b] Note that there are no fragments or study sites within the size class of 150-200 ha, which would have corresponded to 5 transects.

APPENDIX IV

CLASSIFICATION OF BIRD SPECIES INCLUDED IN ANALYSIS

Species[a]		Seasonal Status[b]	Diet	Foraging guild[c] Substrate and technique
Anna's Hummingbird	*Calypte anna*	Resident	nectar	hover & glean
Rufous Hummingbird	*Selasphorus rufus*	Migrant	nectar	hover & glean
Downy Woodpecker	*Picoides pubescens*	Resident	insects	bark glean
Hairy Woodpecker	*Picoides villosus*	Resident	insects	bark glean
Northern Flicker	*Colaptes auratus*	Resident	insects	bark glean
Pileated Woodpecker	*Dryocopus pileatus*	Resident	insects	bark glean
Olive-sided Flycatcher	*Contopus cooperi*	Migrant	insects	hawks
Hammond's Flycatcher	*Empidonax hammondii*	Migrant	insects	hawks
Pacific-slope Flycatcher	*Empidonax difficilis*	Migrant	insects	hawks
Cassin's Vireo	*Vireo cassinii*	Migrant	insects	foliage glean
Hutton's Vireo	*Vireo huttoni*	Resident	insects	foliage glean
Warbling Vireo	*Vireo gilvus*	Migrant	insects	foliage glean
Red-eyed Vireo	*Vireo olivaceus*	Migrant	insects	hover & glean
Stellar's Jay	*Cyanocitta stelleri*	Resident	omnivore	ground glean
Northwestern Crow	*Corvus caurinus*	Resident	omnivore	ground glean
Common Raven	*Corvus corax*	Resident	omnivore	ground glean
Black-capped Chickadee	*Poecile atricapillus*	Resident	insects	foliage glean
Chestnut-backed Chickadee	*Poecile rufescens*	Resident	insects	foliage glean
Bushtit	*Psaltriparus minimus*	Resident	insects	foliage glean
Red-breasted Nuthatch	*Sitta canadensis*	Resident	insects	bark glean
Brown Creeper	*Certhia americana*	Resident	insects	bark glean
Bewick's Wren	*Thryomanes bewickii*	Resident	insects	ground glean
Winter Wren	*Troglodytes troglodytes*	Resident	insects	ground glean
Golden-crowned Kinglet	*Regulus satrapa*	Resident	insects	foliage glean
Ruby-crowned Kinglet	*Regulus calendula*	Migrant	insects	foliage glean
Swainson's Thrush	*Catharus ustulatus*	Migrant	insects	foliage glean
Hermit Thrush	*Catharus guttatus*	Migrant	insects	ground glean
American Robin	*Turdus migratorius*	Resident	insects	ground glean
Varied Thrush	*Ixoreus naevius*	Resident	insects	ground glean
European Starling	*Sturnus vulgaris*	Resident	insects	ground glean
Cedar Waxwing	*Bombycilla cedrorum*	Migrant	fruit	foliage glean
Orange-crowned Warbler	*Vermivora celata*	Migrant	insects	foliage glean
Yellow Warbler	*Dendroica petechia*	Migrant	insects	foliage glean
Yellow-rumped Warbler	*Dendroica coronata*	Migrant	insects	foliage glean
Black-throated Gray Warbler	*Dendroica nigrescens*	Migrant	insects	foliage glean

Continued.

Species		Seasonal Status	Diet	Foraging guild Substrate and technique
Townsend's Warbler	*Dendroica townsendi*	Migrant	insects	foliage glean
Wilson's Warbler	*Wilsonia pusilla*	Migrant	insects	foliage glean
Western Tanager	*Piranga ludoviciana*	Migrant	insects	foliage glean
Black-headed Grosbeak	*Pheucticus melanocephalus*	Migrant	insects	foliage glean
Spotted Towhee	*Pipilo maculatus*	Resident	insects	ground glean
Fox Sparrow	*Passerella iliaca*	Migrant	insects	ground glean
Song Sparrow	*Melospiza melodia*	Resident	insects	ground glean
Dark-eyed Junco	*Junco hyemalis*	Resident	seeds	ground glean
Brown-headed Cowbird	*Molothrus ater*	Migrant	insects	ground glean
Purple Finch	*Carpodacus purpureus*	Resident	seeds	ground glean
Red Crossbill	*Loxia curvirostra*	Resident	seeds	foliage glean
Pine Siskin	*Carduelis pinus*	Resident	seeds	foliage glean
Evening Grosbeak	*Coccothraustes vespertinus*	Resident	seeds	ground glean

[a] Species names follow the AOU (2000). Species are ordered in taxonomically.
[b] Seasonal status of birds follow Toochin (1998) and Campbell et al. (2001b).
[c] Foraging guild classifications follow Ehrlich et al. (1988).

APPENDIX V

SUMMARY OF BIRD SPECIES DETECTED ACROSS SEASONS

Species[a]		Spr	Sum	Fall	Win	Total (all detections)	Total (detections included in analysis)
Golden-crowned Kinglet	*Regulus satrapa*	86[b]	13	366	413	878	878
Winter Wren	*Troglodytes troglodytes*	214	150	208	198	770	770
Chestnut-backed Chickadee	*Poecile rufescens*	93	172	201	151	617	617
Black-capped Chickadee	*Poecile atricapillus*	104	99	161	150	514	514
Spotted Towhee	*Pipilo maculatus*	79	100	61	53	293	293
Pine Siskin	*Carduelis pinus*	27	24	70	143	264	264
Brown Creeper	*Certhia americana*	34	44	47	41	166	166
Northwestern Crow	*Corvus caurinus*	48	33	46	31	158	158
American Robin	*Turdus migratorius*	55	36	8	28	127	127
Swainson's Thrush	*Catharus ustulatus*	36	88	-	-	124	124
Wilson's Warbler	*Wilsonia pusilla*	41	24	28	-	93	93
Pacific-slope Flycatcher	*Empidonax difficilis*	38	54	-	-	92	92
Red-breasted Nuthatch	*Sitta canadensis*	27	22	29	11	89	89
Yellow-rumped Warbler	*Dendroica coronata*	31	*2*	51	-	84	82
Ruby-crowned Kinglet	*Regulus calendula*	18	-	62	*3*	83	80
Northern Flicker	*Colaptes auratus*	6	8	37	11	62	62
Dark-eyed Junco	*Junco hyemalis*	13	2	18	23	56	56
Hairy Woodpecker	*Picoides villosus*	6	18	16	10	50	50
Varied Thrush	*Ixoreus naevius*	8	-	21	13	42	42
Warbling Vireo	*Vireo gilvus*	19	16	-	-	35	35
Downy Woodpecker	*Picoides pubescens*	12	11	6	5	34	34
Song Sparrow	*Melospiza melodia*	9	4	7	5	25	25
Orange-crowned Warbler	*Vermivora celata*	15	4	5	-	24	24
Yellow Warbler	*Dendroica petechia*	21	-	3	-	24	24
Purple Finch	*Carpodacus purpureus*	9	4	5	3	21	21
Pileated Woodpecker	*Dryocopus pileatus*	8	6	2	3	19	19
Bushtit	*Psaltriparus minimus*	-	*1*	18	-	19	18
Fox Sparrow	*Passerella iliaca*	-	-	7	9	16	16
Black-throated Gray Warbler	*Dendroica nigrescens*	11	2	2	-	15	15

Continued.

Species		Spr	Sum	Fall	Win	Total (all detections)	Total (detections included in analysis)
Evening Grosbeak	*Coccothraustes vespertinus*	2	-	8	4	14	14
Stellar's Jay	*Cyanocitta stelleri*	2	3	4	3	12	12
Townsend's Warbler	*Dendroica townsendi*	9	*1*	3	-	13	12
Black-headed Grosbeak	*Pheucticus melanocephalus*	*1*	10	-	-	11	10
Hutton's Vireo	*Vireo huttoni*	3	5	2	-	10	10
Rufous Hummingbird	*Selasphorus rufus*	6	4	-	-	10	10
Anna's Hummingbird	*Calypte anna*	4	2	-	2	8	8
Bewick's Wren	*Thryomanes bewickii*	7	-	-	-	7	7
Hammond's Flycatcher	*Empidonax hammondii*	7	-	-	-	7	7
Red-eyed Vireo	*Vireo olivaceus*	2	5	-	-	7	7
Cedar Waxwing	*Bombycilla cedrorum*	-	6	-	-	6	6
Hermit Thrush	*Catharus guttatus*	6	-	-	-	6	6
Red Crossbill	*Loxia curvirostra*	-	-	6	-	6	6
Olive-sided Flycatcher	*Contopus cooperi*	3	2	-	-	5	5
Brown-headed Cowbird	*Molothrus ater*	2	2	-	-	4	4
Cassin's Vireo	*Vireo cassinii*	3	-	-	-	3	3
Common Raven	*Corvus corax*	*1*	*1*	*1*	3	6	3
European Starling	*Sturnus vulgaris*	3	-	-	-	3	3
Western Tanager	*Piranga ludoviciana*	3	-	-	-	3	3
Barred Owl	*Strix varia*	*4*	*2*	-	*1*	7	-
MacGilivray's Warbler	*Oporornis tolmiei*	-	*1*	-	-	1	-
White-crowned Sparrow	*Zonotrichia leucophrys*	*1*	-	-	-	1	-
Willow Flycatcher	*Empidonax traillii*	*1*	-	-	-	1	-
	Grand total					4945	4924

[a] Species names follow AOU (2000). Species are ordered in descending order of the number of detections.
[b] Values refer to the number of detections. Italized numbers refer to records that were excluded from the analysis

106

APPENDIX VI

SUMMARY OF BIRD SPECIES RICHNESS AND BIRD DENSITY RECORDED FOR EACH FOREST FRAGMENT ACROSS SEASONS

Table A. Bird species richness, rarefied bird species richness, overall density and resident density across seasons[a]

Sites	Bird species richness (no. of species)				Rarefied bird species richness (expected no. of species)				Overall density (birds/ha)				Resident density (birds/ha)			
	Spr	Sum	Fall	Win	Spr	Sum	Fall	Win	Spr	Sum	Fall	Win	Spr	Sum	Fall	Win
Brockton	9	8	7	9	7.7	7.9	6.9	8.4	4.7	5.3	7.5	7.4	4.7	4.8	6.4	7.4
Campus-S	8	9	7	5	8.0	9.0	6.9	4.9	5.1	3.1	4.1	9.6	4.6	2.6	4.1	9.6
16th-Uni Blvd-N	8	9	6	4	8.0	8.5	6	4	6.3	5.9	3.6	2.0	5.9	4.3	3.0	2.0
Musqueam	13	10	10	6	10.2	9.7	8.7	5.5	9.4	5.9	9.1	10.9	6.6	5.3	8.0	10.9
Shaughnessy	16	12	12	7	10.6	9.2	9.1	5.9	8.9	4.9	7.0	8.3	7.1	4.4	6.8	8.3
W-Park Dr	17	9	14	11	9.9	7.8	9.5	9.3	9.9	6.5	9.3	3.6	8.9	4.7	8.6	3.6
16th-Uni Blvd-S	24	14	6	4	11.5	8.8	8.8	7.5	8.3	6.0	7.9	7.6	6.5	5.2	6.8	7.6
Uni-Chancellor Blvd	19	14	16	9	9.8	9.5	10.7	7.5	8.0	6.5	8.0	5.9	4.7	5.3	6.7	5.9
E-Causeway	25	13	15	9	11.1	8.3	9.9	6.9	9.6	6.6	9.4	6.3	8.1	5.7	6.6	6.0
Lighthouse	23	14	18	14	10.3	9.3	10.6	8.6	10.6	5.4	10.4	10.2	9.0	4.8	8.6	10.2
N-Chancellor Blvd	20	20	15	6	10.7	11.6	9.1	5.5	10.1	7.6	10.2	4.8	7.3	4.7	7.0	4.4
W-Causeway	26	20	20	16	10.6	10.5	10.7	8.4	9.8	7.5	9.5	11.0	7.8	6.4	7.8	10.8
S-16th Ave	32	22	24	18	10.8	9.5	11.2	8.6	9.2	7.0	10.5	10.3	6.8	5.8	8.9	10.0
N-SW Marine	30	21	22	17	11.0	10.7	10.2	7.3	9.4	6.4	12.2	10.4	7.5	5.1	10.9	10.4

[a]Values refer to means across all transects and over two surveys in each season

Table B. Migrant density, insectivore density, granivore density and foliage gleaner density across seasons[a]

Sites	Migrant density (birds/ha)				Insectivore density (birds/ha)				Granivore density (birds/ha)				Foliage gleaner density (birds/ha)			
	Spr	Sum	Fall	Win	Spr	Sum	Fall	Win	Spr	Sum	Fall	Win	Spr	Sum	Fall	Win
Brockton	0.0	1.3	1.0	0.0	3.3	4.2	5.2	6.7	0.0	0.0	0.0	0.0	1.6	2.1	4.7	6.5
Campus-S	0.5	0.6	0.0	0.0	5.1	2.1	4.1	8.3	0.0	0.0	0.0	0.0	3.0	0.5	1.0	6.7
16th-Uni Blvd-N	0.6	2.4	1.2	0.0	5.1	4.8	3.6	2.0	0.0	0.0	0.0	0.0	3.0	2.7	2.0	0.0
Musqueam	2.9	1.3	2.5	0.0	8.9	6.1	9.1	10.9	0.0	0.0	0.0	0.0	5.6	3.5	5.8	10.6
Shaughnessy	2.9	0.5	0.6	0.0	8.3	4.6	6.7	8.3	0.9	0.6	0.6	0.0	6.1	2.1	2.3	4.9
W-Park Dr	1.5	3.0	1.2	0.0	8.9	5.4	9.0	3.3	0.6	0.0	0.0	0.0	3.2	2.1	5.4	1.0
16th-Uni Blvd-S	3.1	0.9	2.5	0.0	7.7	6.0	7.8	7.0	0.4	0.0	0.0	1.2	4.3	2.7	5.4	4.6
Uni-Chancellor Blvd	3.8	1.3	2.3	0.0	7.7	6.3	7.9	5.9	0.4	0.0	0.0	0.0	4.1	3.9	5.4	2.9
E-Causeway	2.1	1.3	2.0	0.0	9.0	6.2	8.9	5.8	0.8	0.0	0.0	0.4	6.2	4.1	6.8	3.1
Lighthouse	2.9	1.7	3.2	0.0	9.8	5.1	7.9	6.7	1.9	0.8	2.7	4.1	5.6	3.4	5.4	6.6
N-Chancellor Blvd	3.1	3.0	5.0	0.8	9.9	7.2	10.2	4.4	0.0	0.0	0.0	0.0	4.9	2.8	7.5	0.7
W-Causeway	2.5	1.8	2.2	0.6	8.4	7.0	8.7	8.8	1.5	0.9	0.4	3.3	5.8	5.2	5.2	7.4
S-16th Ave	3.5	1.4	2.6	0.5	8.5	6.1	9.6	7.2	1.0	0.4	1.8	1.8	4.7	3.2	6.3	6.5
N-SW Marine	2.4	1.3	2.2	0.0	8.3	5.9	11.5	9.3	1.2	0.8	1.0	1.3	5.4	3.8	7.5	6.7

[a]Values refer to means across all transects and over two surveys in each season

Table C. Bark gleaner density and hawker density across seasons[a]

Sites	Ground gleaner density (birds/ha)				Bark gleaner density (birds/ha)				Hawker density (birds/ha)			
	Spr	Sum	Fall	Win	Spr	Sum	Fall	Win	Spr	Sum	Fall	Win
Brockton	3.2	2.7	3.1	3.7	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0
Campus-S	3.3	2.1	3.2	2.1	0.0	0.0	0.0	1.2	0.0	1.3	0.0	0.0
16th-Uni Blvd-N	3.4	3.4	1.0	1.7	0.0	0.5	1.2	1.2	0.0	0.0	0.0	0.0
Musqueam	3.4	1.6	2.7	0.5	0.0	1.2	1.2	0.0	0.0	0.0	0.0	0.0
Shaughnessy	3.6	2.0	4.1	3.5	2.5	1.8	2.1	1.8	0.6	0.0	0.0	0.0
W-Park Dr	6.3	4.1	3.7	1.5	0.9	0.6	0.8	1.8	0.3	0.0	0.0	0.0
16th-Uni Blvd-S	3.4	2.8	2.4	2.6	0.5	1.5	0.6	0.5	0.0	0.6	0.0	0.0
Uni-Chancellor Blvd	2.7	2.0	2.3	2.0	1.0	1.4	2.0	1.1	1.4	0.8	0.0	0.0
E-Causeway	4.7	2.3	2.5	2.8	0.2	0.8	0.3	0.4	0.8	0.4	0.0	0.0
Lighthouse	4.8	1.7	3.7	3.0	1.7	1.7	3.0	2.1	0.4	0.0	0.0	0.0
N-Chancellor Blvd	3.7	3.1	2.0	3.7	2.2	2.0	1.2	1.2	0.2	1.9	0.0	0.0
W-Causeway	2.8	1.9	4.5	3.5	0.9	1.4	1.3	1.0	1.4	0.5	0.0	0.0
S-16th Ave	3.3	3.0	3.5	3.9	1.4	1.8	1.6	0.8	1.2	0.3	0.0	0.0
N-SW Marine	4.0	2.0	3.4	2.8	0.8	1.3	2.6	1.6	0.5	0.3	0.0	0.0

[a]Values refer to means across all transects and over two surveys in each season

APPENDIX VII

SUMMARY OF HABITAT VARIABLES RECORDED FOR EACH FOREST FRAGMENT[a]

	Conifer	Decid	TSD	DBH	TrDen	MTCond	ShDen	ShSD	UnCov	OvCov	TotCov	FHD	HH
Brockton	0.71	0.29	0.96	39.7	262.5	1.73	2.3	1.04	0.37	0.28	2.19	1.67	0.36
Campus-S	0.86	0.14	0.93	43.5	318.8	1.68	1.5	1.48	0.58	0.27	2.66	1.68	0.30
16th-Uni Blvd-N	0.47	0.53	1.07	38.1	387.5	1.65	3.0	1.79	0.70	0.23	2.78	1.71	0.26
Musqueam	0.83	0.17	1.21	49.6	287.5	1.76	1.4	1.93	0.79	0.32	3.48	1.80	0.29
Shaughnessy	0.75	0.25	1.12	43.5	290.6	1.81	1.4	1.25	0.64	0.25	2.79	1.61	0.22
W-Park Dr	0.35	0.65	1.22	50.4	187.5	1.74	1.4	1.38	0.54	0.28	2.63	1.70	0.22
16th-Uni Blvd-S	0.67	0.33	1.15	46.5	325.0	1.65	1.4	1.61	0.61	0.38	3.15	1.72	0.28
Uni-Chancellor Blvd	0.41	0.59	1.23	39.5	443.8	2.03	2.5	1.96	0.70	0.29	3.00	1.72	0.19
E-Causeway	0.62	0.38	1.15	41.9	245.8	1.52	2.8	1.37	0.63	0.31	2.99	1.77	0.32
Lighthouse[b]	0.90	0.09	1.07	43.2	337.5	1.78	1.5	1.31	0.31	0.29	2.13	1.82	0.21
N-Chancellor Blvd	0.18	0.82	1.31	30.8	508.3	1.91	2.3	1.77	0.81	0.35	3.68	1.71	0.26
W-Causeway	0.69	0.31	1.26	43.6	359.4	2.02	1.6	1.69	0.49	0.36	2.78	1.74	0.36
S-16th Ave	0.82	0.18	1.15	44.9	359.4	1.99	1.8	1.65	0.57	0.37	3.02	1.73	0.26
N-SW Marine	0.82	0.18	1.27	50.9	281.3	1.88	1.5	1.55	0.58	0.34	2.98	1.75	0.24

Conifer: proportion of coniferous trees; Decid: proportion of deciduous broadleaved trees; TSD: tree species diversity (H); DBH: mean tree diameter at breast height (cm); TrDen: tree density (trees/ha); MTCond: mean tree condition (mean decay score); ShDen: shrub density (shrubs/ha); ShSD: shrub species diversity (H); UnCov: proportion of understorey foliage cover; OvCov: proportion of overstorey foliage cover; TotCov: total foliage cover; FHD: foliage height diversity (H); HH: horizontal heterogeneity.

[a]Values refer to means across transects in each fragment.

[b]The proportion of deciduous broadleaved trees and proportion of coniferous trees would add up to 1 in all fragments, except Lighthouse. This is because of the presence of arbutus, which is an evergreen broadleaved tree.

APPENDIX VIII

REGRESSIONS BETWEEN RAREFIED BIRD SPECIES RICHNESS, DENSITY AND HABITAT VARIABLES THAT REMAINED CONSTANT WITH FRAGMENT AREA

	Spring	Summer	Fall	Winter
Rarefied bird species richness	Conifer $R^2 < 0.01$, $F_{1,12} < 0.01$, $p = 0.969$	Conifer $R^2 = 0.01$, $F_{1,12} = 0.11$, $p = 0.744$	Conifer $R^2 = 0.01$, $F_{1,12} = 0.07$, $p = 0.798$	Conifer $R^2 = 0.01$, $F_{1,12} = 0.15$, $p = 0.709$
	Decid $R^2 < 0.01$, $F_{1,12} < 0.01$, $p = 0.967$	Decid $R^2 = 0.26$, $F_{1,12} = 4.19$, $p = 0.744$	Decid $R^2 = 0.01$, $F_{1,12} = 0.07$, $p = 0.794$	Decid $R^2 = 0.01$, $F_{1,12} = 0.15$, $p = 0.704$
	DBH $R^2 = 0.07$, $F_{1,12} = 0.95$, $p = 0.350$	DBH $R^2 = 0.05$, $F_{1,12} = 0.67$, $p = 0.428$	DBH $R^2 = 0.06$, $F_{1,12} = 0.81$, $p = 0.387$	DBH $R^2 = 0.13$, $F_{1,12} = 1.79$, $p = 0.206$
	TrDen $R^2 < 0.01$, $F_{1,12} = 0.01$, $p = 0.914$	TrDen (+) $R^2 = \mathbf{0.42}$, $F_{1,12} = \mathbf{8.65^*}$, $p = 0.012$	TrDen $R^2 = 0.01$, $F_{1,12} = 0.08$, $p = 0.782$	TrDen $R^2 = 0.11$, $F_{1,12} = 1.54$, $p = 0.238$
	ShDen $R^2 = 0.11$, $F_{1,12} = 1.49$, $p = 0.245$	ShDen $R^2 = 0.02$, $F_{1,12} = 0.25$, $p = 0.627$	ShDen $R^2 = 0.08$, $F_{1,12} = 1.00$, $p = 0.337$	ShDen $R^2 = 0.10$, $F_{1,12} = 1.29$, $p = 0.279$
	ShSD $R^2 = 0.04$, $F_{1,12} = 0.45$, $p = 0.517$	ShSD $R^2 = 0.26$, $F_{1,12} = 4.27$, $p = 0.061$	ShSD $R^2 = 0.03$, $F_{1,12} = 0.31$, $p = 0.588$	ShSD $R^2 = 0.13$, $F_{1,12} = 1.82$, $p = 0.203$
	UnCov $R^2 = 0.03$, $F_{1,12} = 0.40$, $p = 0.539$	UnCov $R^2 = 0.14$, $F_{1,12} = 1.89$, $p = 0.194$	UnCov $R^2 = 0.02$, $F_{1,12} = 0.20$, $p = 0.660$	UnCov (-) $R^2 = \mathbf{0.45}$, $F_{1,12} = 9.90^*$, $p = 0.008$
	TotCov $R^2 = 0.24$, $F_{1,12} = 3.79$, $p = 0.075$	TotCov (+) $R^2 = \mathbf{0.34}$, $F_{1,12} = \mathbf{6.09^*}$, $p = 0.030$	TotCov $R^2 = 0.02$, $F_{1,12} = 0.27$, $p = 0.611$	TotCov $R^2 = 0.17$, $F_{1,12} = 2.51$, $p = 0.139$
	FHD $R^2 = 0.12$, $F_{1,12} = 1.67$, $p = 0.221$	FHD $R^2 = 0.04$, $F_{1,12} = 0.52$, $p = 0.484$	FHD $R^2 = 0.17$, $F_{1,12} = 2.49$, $p = 0.140$	FHD $R^2 = 0.04$, $F_{1,12} = 0.45$, $p = 0.517$
	HH $R^2 = 0.05$, $F_{1,12} = 0.63$, $p = 0.444$	HH $R^2 = 0.01$, $F_{1,12} = 0.10$, $p = 0.754$	HH $R^2 = 0.09$, $F_{1,12} = 1.22$, $p = 0.291$	HH $R^2 < 0.01$, $F_{1,12} < 0.01$, $p = 0.999$

Continued.

	Spring	Summer	Fall	Winter
Overall bird density	Conifer $R^2 = 0.01$, $F_{1,12} = 0.15$, p = 0.700	Conifer $R^2 = 0.26$, $F_{1,12} = 4.19$, p = 0.063	Conifer $R^2 < 0.01$, $F_{1,12} = 0.04$, p = 0.847	Conifer (+) $R^2 = \mathbf{0.68}$, $F_{1,12} = 26.07^*$, p < 0.001
	Decid $R^2 = 0.01$, $F_{1,12} = 0.15$, p = 0.707	Decid $R^2 = 0.26$, $F_{1,12} = 4.19$, p = 0.063	Decid $R^2 < 0.01$, $F_{1,12} = 0.04$, p = 0.843	Decid (-) $R^2 = \mathbf{0.68}$, $F_{1,12} = 26.02^*$, p < 0.001
	DBH $R^2 = 0.05$, $F_{1,12} = 0.59$, p = 0.457	DBH $R^2 = 0.02$, $F_{1,12} = 0.29$, p = 0.599	DBH $R^2 = 0.08$, $F_{1,12} = 1.01$, p = 0.335	DBH $R^2 = 0.21$, $F_{1,12} = 3.22$, p = 0.098
	TrDen $R^2 < 0.01$, $F_{1,12} = 0.02$, p = 0.888	TrDen $R^2 = 0.10$, $F_{1,12} = 1.36$, p = 0.266	TrDen $R^2 < 0.01$, $F_{1,12} = 0.04$, p = 0.842	TrDen $R^2 = 0.02$, $F_{1,12} = 0.26$, p = 0.621
	ShDen $R^2 = 0.09$, $F_{1,12} = 1.18$, p = 0.299	ShDen $R^2 = 0.07$, $F_{1,12} = 0.91$, p = 0.359	ShDen $R^2 = 0.09$, $F_{1,12} = 1.13$, p = 0.309	ShDen (-) $R^2 = \mathbf{0.41}$, $F_{1,12} = 8.28^*$, p = 0.014
	ShSD $R^2 = 0.04$, $F_{1,12} = 0.54$, p = 0.476	ShSD $R^2 = 0.17$, $F_{1,12} = 2.42$, p = 0.146	ShSD $R^2 < 0.01$, $F_{1,12} < 0.01$, p = 0.981	ShSD $R^2 < 0.01$, $F_{1,12} = 0.05$, p = 0.830
	UnCov $R^2 = 0.01$, $F_{1,12} = 0.12$, p = 0.734	UnCov $R^2 = 0.05$, $F_{1,12} = 0.68$, p = 0.425	UnCov $R^2 = 0.02$, $F_{1,12} = 0.24$, p = 0.630	UnCov $R^2 = 0.10$, $F_{1,12} = 1.37$, p = 0.265
	TotCov $R^2 = 0.12$, $F_{1,12} = 1.61$, p = 0.229	TotCov $R^2 = 0.22$, $F_{1,12} = 3.29$, p = 0.095	TotCov $R^2 = 0.05$, $F_{1,12} = 0.58$, p = 0.460	TotCov $R^2 < 0.01$, $F_{1,12} = 0.05$, p = 0.830
	FHD $R^2 = 0.24$, $F_{1,12} = 3.83$, p = 0.074	FHD $R^2 = 0.09$, $F_{1,12} = 1.18$, p = 0.199	FHD $R^2 = 0.25$, $F_{1,12} = 3.92$, p = 0.071	FHD $R^2 = 0.12$, $F_{1,12} = 1.67$, p = 0.221
	HH $R^2 = 0.12$, $F_{1,12} = 1.71$, p = 0.215	HH $R^2 < 0.01$, $F_{1,12} < 0.01$, p = 0.967	HH $R^2 = 0.01$, $F_{1,12} = 0.15$, p = 0.707	HH $R^2 = 0.06$, $F_{1,12} = 0.75$, p = 0.404

Continued.

	Spring	Summer	Fall	Winter
Resident density	Conifer $R^2 < 0.01$, $F_{1,12} < 0.01$, $p = 0.917$	Conifer $R^2 < 0.01$, $F_{1,12} = 0.02$, $p = 0.890$	Conifer $R^2 = 0.05$, $F_{1,12} = 0.64$, $p = 0.440$	Conifer (+) $R^2 = \mathbf{0.71}$, $F_{1,12} = 29.11^*$, $p < 0.001$
	Decid $R^2 < 0.01$, $F_{1,12} < 0.01$, $p = 0.926$	Decid $R^2 < 0.01$, $F_{1,12} = 0.02$, $p = 0.889$	Decid $R^2 = 0.05$, $F_{1,12} = 0.65$, $p = 0.437$	Decid (-) $R^2 = \mathbf{0.71}$, $F_{1,12} = 29.06^*$, $p < 0.001$
	DBH $R^2 = 0.09$, $F_{1,12} = 1.16$, $p = 0.304$	DBH $R^2 = 0.02$, $F_{1,12} = 0.22$, $p = 0.648$	DBH (+) $R^2 = 0.29$, $F_{1,12} = 4.93$, $p = 0.047$	DBH $R^2 = 0.23$, $F_{1,12} = 3.64$, $p = 0.081$
	TrDen $R^2 = 0.08$, $F_{1,12} = 1.02$, $p = 0.333$	TrDen $R^2 < 0.01$, $F_{1,12} = 0.01$, $p = 0.911$	TrDen $R^2 = 0.06$, $F_{1,12} = 0.76$, $p = 0.399$	TrDen $R^2 = 0.03$, $F_{1,12} = 0.34$, $p = 0.573$
	ShDen $R^2 = 0.10$, $F_{1,12} = 1.26$, $p = 0.284$	ShDen $R^2 = 0.01$, $F_{1,12} = 0.10$, $p = 0.754$	ShDen $R^2 = 0.27$, $F_{1,12} = 4.54$, $p = 0.054$	ShDen (-) $R^2 = \mathbf{0.43}$, $F_{1,12} = 8.97^*$, $p = 0.011$
	ShSD $R^2 = 0.03$, $F_{1,12} = 0.38$, $p = 0.550$	ShSD $R^2 = 0.05$, $F_{1,12} = 0.68$, $p = 0.426$	ShSD $R^2 < 0.01$, $F_{1,12} = 0.05$, $p = 0.833$	ShSD $R^2 = 0.01$, $F_{1,12} = 0.06$, $p = 0.808$
	UnCov $R^2 = 0.04$, $F_{1,12} = 0.55$, $p = 0.472$	UnCov $R^2 < 0.01$, $F_{1,12} = 0.02$, $p = 0.878$	UnCov $R^2 = 0.05$, $F_{1,12} = 0.67$, $p = 0.430$	UnCov $R^2 = 0.11$, $F_{1,12} = 1.49$, $p = 0.246$
	TotCov $R^2 < 0.01$, $F_{1,12} < 0.01$, $p = 0.957$	TotCov $R^2 = 0.05$, $F_{1,12} = 0.65$, $p = 0.437$	TotCov $R^2 = 0.01$, $F_{1,12} = 0.09$, $p = 0.770$	TotCov $R^2 = 0.01$, $F_{1,12} = 0.09$, $p = 0.767$
	FHD $R^2 = 0.16$, $F_{1,12} = 2.35$, $p = 0.151$	FHD $R^2 = 0.19$, $F_{1,12} = 2.83$, $p = 0.119$	FHD $R^2 = 0.15$, $F_{1,12} = 2.12$, $p = 0.171$	FHD $R^2 = 0.12$, $F_{1,12} = 1.59$, $p = 0.231$
	HH $R^2 = 0.04$, $F_{1,12} = 0.52$, $p = 0.483$	HH $R^2 = 0.04$, $F_{1,12} = 0.49$, $p = 0.496$	HH $R^2 = 0.04$, $F_{1,12} = 0.56$, $p = 0.468$	HH $R^2 = 0.05$, $F_{1,12} = 0.66$, $p = 0.434$

Continued.

	Spring	Summer	Fall	Winter
Migrant density	Conifer $R^2 < 0.01$, $F_{1,12} = 0.02$, $p = 0.876$	Conifer (-) $R^2 = \textbf{0.54}$, $F_{1,12} = 13.88^*$, $p = 0.003$	Conifer $R^2 = 0.12$, $F_{1,12} = 1.57$, $p = 0.234$	Insufficient data
	Decid $R^2 < 0.01$, $F_{1,12} = 0.02$, $p = 0.880$	Decid (+) $R^2 = \textbf{0.53}$, $F_{1,12} = 13.69^*$, $p = 0.003$	Decid $R^2 = 0.11$, $F_{1,12} = 1.54$, $p = 0.239$	
	DBH $R^2 < 0.01$, $F_{1,12} = 0.04$, $p = 0.842$	DBH $R^2 = 0.09$, $F_{1,12} = 1.18$, $p = 0.299$	DBH $R^2 = 0.12$, $F_{1,12} = 1.68$, $p = 0.219$	
	TrDen $R^2 = 0.16$, $F_{1,12} = 2.33$, $p = 0.153$	TrDen $R^2 = 0.05$, $F_{1,12} = 0.69$, $p = 0.422$	TrDen (+) $R^2 = \textbf{0.35}$, $F_{1,12} = 6.59^*$, $p = 0.025$	
	ShDen $R^2 = 0.05$, $F_{1,12} = 0.66$, $p = 0.433$	ShDen $R^2 = 0.09$, $F_{1,12} = 1.15$, $p = 0.304$	ShDen $R^2 = 0.01$, $F_{1,12} = 0.12$, $p = 0.734$	
	ShSD $R^2 = 0.23$, $F_{1,12} = 3.55$, $p = 0.084$	ShSD $R^2 = 0.05$, $F_{1,12} = 0.60$, $p = 0.453$	ShSD $R^2 = 0.18$, $F_{1,12} = 2.67$, $p = 0.128$	
	UnCov $R^2 = 0.09$, $F_{1,12} = 1.22$, $p = 0.290$	UnCov $R^2 = 0.02$, $F_{1,12} = 0.23$, $p = 0.643$	UnCov $R^2 = 0.06$, $F_{1,12} = 0.81$, $p = 0.386$	
	TotCov $R^2 = 0.27$, $F_{1,12} = 4.50$, $p = 0.055$	TotCov $R^2 = 0.02$, $F_{1,12} = 0.26$, $p = 0.619$	TotCov (+) $R^2 = \textbf{0.28}$, $F_{1,12} = 4.77^*$, $p = 0.0495$	
	FHD $R^2 = 0.11$, $F_{1,12} = 1.45$, $p = 0.252$	FHD $R^2 = 0.02$, $F_{1,12} = 0.19$, $p = 0.671$	FHD $R^2 = 0.26$, $F_{1,12} = 4.25$, $p = 0.062$	
	HH $R^2 = 0.22$, $F_{1,12} = 3.39$, $p = 0.091$	HH $R^2 = 0.02$, $F_{1,12} = 0.26$, $p = 0.621$	HH $R^2 = 0.02$, $F_{1,12} = 0.26$, $p = 0.616$	

Continued.

	Spring	Summer	Fall	Winter
Insectivore density	Conifer $R^2 = 0.02$, $F_{1,12} = 0.20$, p = 0.653	Conifer $R^2 = 0.17$, $F_{1,12} = 2.39$, p = 0.147	Conifer $R^2 = 0.01$, $F_{1,12} = 0.11$, p = 0.746	Conifer (+) $R^2 = \mathbf{0.55}$, $F_{1,12} = 14.58^*$, p = 0.002
	Decid $R^2 = 0.02$, $F_{1,12} = 0.20$, p = 0.660	Decid $R^2 = 0.17$, $F_{1,12} = 2.39$, p = 0.148	Decid $R^2 = 0.01$, $F_{1,12} = 0.11$, p = 0.747	Decid (-) $R^2 = \mathbf{0.55}$, $F_{1,12} = 14.41^*$, p = 0.003
	DBH $R^2 = 0.03$, $F_{1,12} = 0.32$, p = 0.581	DBH $R^2 < 0.01$, $F_{1,12} = 0.11$, p = 0.746	DBH $R^2 = 0.09$, $F_{1,12} = 1.13$, p = 0.309	DBH $R^2 = 0.24$, $F_{1,12} = 3.89$, p = 0.072
	TrDen $R^2 = 0.01$, $F_{1,12} = 0.17$, p = 0.684	TrDen $R^2 = 0.12$, $F_{1,12} = 1.63$, p = 0.225	TrDen $R^2 < 0.01$, $F_{1,12} < 0.01$, p = 0.954	TrDen $R^2 = 0.04$, $F_{1,12} = 0.52$, p = 0.485
	ShDen $R^2 = 0.09$, $F_{1,12} = 1.25$, p = 0.285	ShDen $R^2 = 0.02$, $F_{1,12} = 0.27$, p = 0.616	ShDen $R^2 = 0.08$, $F_{1,12} = 1.05$, p = 0.326	ShDen (-) $R^2 = \mathbf{0.38}$, $F_{1,12} = 7.47^*$, p = 0.018
	ShSD $R^2 = 0.07$, $F_{1,12} = 0.96$, p = 0.346	ShSD $R^2 = 0.24$, $F_{1,12} = 3.80$, p = 0.075	ShSD $R^2 = 0.06$, $F_{1,12} = 0.71$, p = 0.415	ShSD $R^2 < 0.01$, $F_{1,12} < 0.01$, p = 0.957
	UnCov $R^2 = 0.05$, $F_{1,12} = 0.59$, p = 0.459	UnCov $R^2 = 0.10$, $F_{1,12} = 1.36$, p = 0.267	UnCov $R^2 = 0.03$, $F_{1,12} = 0.34$, p = 0.569	UnCov $R^2 < 0.01$, $F_{1,12} = 0.06$, p = 0.814
	TotCov $R^2 = 0.20$, $F_{1,12} = 2.91$, p = 0.114	TotCov (+) $R^2 = \mathbf{0.33}$, $F_{1,12} = 5.97^*$, p = 0.031	TotCov $R^2 = 0.24$, $F_{1,12} = 3.85$, p = 0.073	TotCov $R^2 = 0.01$, $F_{1,12} = 0.17$, p = 0.690
	FHD $R^2 = 0.22$, $F_{1,12} = 3.44$, p = 0.089	FHD $R^2 = 0.17$, $F_{1,12} = 2.43$, p = 0.145	FHD $R^2 = 0.19$, $F_{1,12} = 2.87$, p = 0.116	FHD $R^2 = 0.05$, $F_{1,12} = 0.62$, p = 0.445
	HH $R^2 = 0.17$, $F_{1,12} = 2.54$, p = 0.137	HH $R^2 < 0.01$, $F_{1,12} = 0.03$, p = 0.876	HH $R^2 = 0.04$, $F_{1,12} = 0.44$, p = 0.521	HH $R^2 = 0.07$, $F_{1,12} = 0.85$, p = 0.375

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	Spring	Summer	Fall	Winter
Granivore density	Conifer $R^2 = 0.17$, $F_{1,12} = 2.43$, $p = 0.145$	Insufficient data	Insufficient data	Insufficient data
	Decid $R^2 = 0.17$, $F_{1,12} = 2.48$, $p = 0.141$			
	DBH $R^2 = 0.11$, $F_{1,12} = 1.44$, $p = 0.254$			
	TrDen $R^2 = 0.02$, $F_{1,12} = 0.28$, $p = 0.607$			
	ShDen $R^2 = 0.11$, $F_{1,12} = 1.48$, $p = 0.247$			
	ShSD $R^2 = 0.06$, $F_{1,12} = 0.74$, $p = 0.408$			
	UnCov (-) $R^2 = \mathbf{0.33}$, $F_{1,12} = 6.04^*$, $p = 0.030$			
	TotCov $R^2 = 0.14$, $F_{1,12} = 1.91$, $p = 0.193$			
	FHD $R^2 = 0.14$, $F_{1,12} = 1.95$, $p = 0.188$			
	HH $R^2 = 0.03$, $F_{1,12} = 0.38$, $p = 0.547$			

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	Spring	Summer	Fall	Winter
Foliage gleaner density	Conifer $R^2 = 0.05$, $F_{1,12} = 0.64$, p = 0.440	Conifer $R^2 < 0.01$, $F_{1,12} < 0.01$, p = 0.942	Conifer $R^2 = 0.04$, $F_{1,12} = 0.51$, p = 0.491	Conifer (+) $R^2 = \mathbf{0.71}$, $F_{1,12} = 28.78^*$, p < 0.001
	Decid $R^2 = 0.05$, $F_{1,12} = 0.65$, p = 0.437	Decid $R^2 < 0.01$, $F_{1,12} < 0.01$, p = 0.944	Decid $R^2 = 0.04$, $F_{1,12} = 0.50$, p = 0.493	Decid (-) $R^2 = \mathbf{0.70}$, $F_{1,12} = 28.57^*$, p < 0.001
	DBH $R^2 = 0.03$, $F_{1,12} = 0.37$, p = 0.553	DBH $R^2 = 0.01$, $F_{1,12} = 0.04$, p = 0.850	DBH $R^2 = 0.01$, $F_{1,12} = 0.07$, p = 0.800	DBH $R^2 = 0.26$, $F_{1,12} = 4.21$, p = 0.063
	TrDen $R^2 < 0.01$, $F_{1,12} = 0.05$, p = 0.829	TrDen $R^2 = 0.03$, $F_{1,12} = 0.42$, p = 0.527	TrDen $R^2 = 0.01$, $F_{1,12} = 0.08$, p = 0.782	TrDen $R^2 = 0.07$, $F_{1,12} = 0.97$, p = 0.345
	ShDen $R^2 = 0.06$, $F_{1,12} = 0.80$, p = 0.389	ShDen $R^2 = 0.03$, $F_{1,12} = 0.35$, p = 0.567	ShDen $R^2 < 0.01$, $F_{1,12} < 0.01$, p = 0.956	ShDen (-) $R^2 = \mathbf{0.34}$, $F_{1,12} = 6.06^*$, p = 0.030
	ShSD $R^2 = 0.04$, $F_{1,12} = 0.47$, p = 0.507	ShSD $R^2 = 0.15$, $F_{1,12} = 2.06$, p = 0.177	ShSD $R^2 = 0.03$, $F_{1,12} = 0.40$, p = 0.539	ShSD $R^2 < 0.01$, $F_{1,12} = 0.05$, p = 0.833
	UnCov $R^2 = 0.04$, $F_{1,12} = 0.47$, p = 0.505	UnCov $R^2 < 0.01$, $F_{1,12} < 0.01$, p = 0.965	UnCov $R^2 = 0.01$, $F_{1,12} = 0.07$, p = 0.789	UnCov $R^2 = 0.08$, $F_{1,12} = 1.03$, p = 0.329
	TotCov $R^2 = 0.14$, $F_{1,12} = 2.02$, p = 0.181	TotCov $R^2 = 0.05$, $F_{1,12} = 0.62$, p = 0.446	TotCov $R^2 = 0.17$, $F_{1,12} = 2.46$, p = 0.143	TotCov $R^2 = 0.01$, $F_{1,12} = 0.12$, p = 0.740
	FHD $R^2 = 0.18$, $F_{1,12} = 2.64$, p = 0.131	FHD (+) $R^2 = \mathbf{0.36}$, $F_{1,12} = 6.61^*$, p = 0.025	FHD (+) $R^2 = \mathbf{0.29}$, $F_{1,12} = 4.84^*$, p = 0.048	FHD $R^2 = 0.12$, $F_{1,12} = 1.70$, p = 0.217
	HH $R^2 = 0.02$, $F_{1,12} = 0.27$, p = 0.610	HH $R^2 = 0.01$, $F_{1,12} = 0.17$, p = 0.068	HH $R^2 < 0.01$, $F_{1,12} < 0.01$, p = 0.984	HH $R^2 = 0.12$, $F_{1,12} = 1.71$, p = 0.216

117

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Ground gleaner density	Spring	Summer	Fall	Winter
	Conifer $R^2 = 0.03$, $F_{1,12} = 0.38$, p = 0.551	Conifer $R^2 = \mathbf{0.40}$, $F_{1,12} = 7.93^*$, p = 0.015	Conifer $R^2 = 0.24$, $F_{1,12} = 3.86$, p = 0.073	Conifer $R^2 < 0.01$, $F_{1,12} = 0.06$, p = 0.813
	Decid $R^2 = 0.03$, $F_{1,12} = 0.36$, p = 0.558	Decid $R^2 = \mathbf{0.40}$, $F_{1,12} = 7.96^*$, p = 0.015	Decid $R^2 = 0.24$, $F_{1,12} = 3.87$, p = 0.073	Decid $R^2 < 0.01$, $F_{1,12} = 0.06$, p = 0.812
	DBH $R^2 = 0.12$, $F_{1,12} = 1.59$, p = 0.231	DBH $R^2 = 0.02$, $F_{1,12} = 0.26$, p = 0.622	DBH $R^2 = 0.24$, $F_{1,12} = 3.84$, p = 0.074	DBH $R^2 = 0.16$, $F_{1,12} = 2.34$, p = 0.152
	TrDen (-) $R^2 = \mathbf{0.32}$, $F_{1,12} = 5.65^*$, p = 0.035	TrDen $R^2 < 0.01$, $F_{1,12} = 0.04$, p = 0.837	TrDen $R^2 = 0.18$, $F_{1,12} = 2.70$, p = 0.126	TrDen $R^2 = 0.06$, $F_{1,12} = 0.76$, p = 0.399
	ShDen $R^2 = 0.04$, $F_{1,12} = 0.50$, p = 0.493	ShDen $R^2 = 0.07$, $F_{1,12} = 0.92$, p = 0.357	ShDen (-) $R^2 = \mathbf{0.50}$, $F_{1,12} = 12.23^*$, p = 0.004	ShDen $R^2 = 0.01$, $F_{1,12} = 0.06$, p = 0.806
	ShSD $R^2 = 0.17$, $F_{1,12} = 2.39$, p = 0.148	ShSD $R^2 = 0.01$, $F_{1,12} = 0.06$, p = 0.807	ShSD $R^2 = 0.21$, $F_{1,12} = 3.18$, p = 0.100	ShSD $R^2 = 0.19$, $F_{1,12} = 2.85$, p = 0.117
	UnCov $R^2 = 0.06$, $F_{1,12} = 0.71$, p = 0.417	UnCov $R^2 < 0.01$, $F_{1,12} = 0.11$, p = 0.743	UnCov (-) $R^2 = \mathbf{0.33}$, $F_{1,12} = 6.04^*$, p = 0.030	UnCov $R^2 = 0.15$, $F_{1,12} = 2.07$, p = 0.176
	TotCov $R^2 = 0.06$, $F_{1,12} = 0.70$, p = 0.419	TotCov $R^2 < 0.01$, $F_{1,12} < 0.01$, p = 0.923	TotCov $R^2 = 0.16$, $F_{1,12} = 2.28$, p = 0.157	TotCov $R^2 = 0.03$, $F_{1,12} = 0.38$, p = 0.549
	FHD $R^2 = 0.03$, $F_{1,12} = 0.33$, p = 0.576	FHD $R^2 = 0.14$, $F_{1,12} = 1.90$, p = 0.193	FHD $R^2 = 0.01$, $F_{1,12} = 0.07$, p = 0.803	FHD $R^2 = 0.09$, $F_{1,12} = 1.15$, p = 0.304
	HH $R^2 = 0.10$, $F_{1,12} = 1.36$, p = 0.267	HH $R^2 = 0.01$, $F_{1,12} = 0.14$, p = 0.714	HH $R^2 = 0.01$, $F_{1,12} = 0.07$, p = 0.795	HH $R^2 = 0.05$, $F_{1,12} = 0.66$, p = 0.432

Continued.

	Spring	Summer	Fall	Winter
Bark gleaner density	Conifer $R^2 = 0.03$, $F_{1,12} = 0.43$, $p = 0.527$	Conifer $R^2 < 0.01$, $F_{1,12} < 0.01$, $p = 0.940$	Conifer $R^2 = 0.03$, $F_{1,12} = 0.39$, $p = 0.544$	Conifer $R^2 = 0.01$, $F_{1,12} = 0.09$, $p = 0.770$
	Decid $R^2 = 0.03$, $F_{1,12} = 0.41$, $p = 0.533$	Decid $R^2 < 0.01$, $F_{1,12} < 0.01$, $p = 0.945$	Decid $R^2 = 0.03$, $F_{1,12} = 0.41$, $p = 0.535$	Decid $R^2 = 0.01$, $F_{1,12} = 0.08$, $p = 0.780$
	DBH $R^2 = 0.06$, $F_{1,12} = 0.79$, $p = 0.391$	DBH $R^2 = 0.05$, $F_{1,12} = 0.59$, $p = 0.458$	DBH $R^2 = 0.02$, $F_{1,12} = 0.24$, $p = 0.635$	DBH $R^2 < 0.01$, $F_{1,12} = 0.04$, $p = 0.839$
	TrDen $R^2 = 0.13$, $F_{1,12} = 1.82$, $p = 0.202$	TrDen $R^2 = 0.17$, $F_{1,12} = 2.41$, $p = 0.146$	TrDen $R^2 = 0.06$, $F_{1,12} = 0.82$, $p = 0.383$	TrDen $R^2 < 0.01$, $F_{1,12} = 0.06$, $p = 0.815$
	ShDen $R^2 = 0.05$, $F_{1,12} = 0.66$, $p = 0.431$	ShDen $R^2 = 0.32$, $F_{1,12} = 2.58$, $p = 0.120$	ShDen $R^2 = 0.05$, $F_{1,12} = 0.66$, $p = 0.431$	ShDen $R^2 = 0.08$, $F_{1,12} = 1.06$, $p = 0.324$
	ShSD $R^2 < 0.01$, $F_{1,12} = 0.07$, $p = 0.800$	ShSD $R^2 < 0.01$, $F_{1,12} = 0.03$, $p = 0.866$	ShSD $R^2 = 0.03$, $F_{1,12} = 0.41$, $p = 0.534$	ShSD $R^2 = 0.02$, $F_{1,12} = 0.24$, $p = 0.632$
	UnCov $R^2 < 0.01$, $F_{1,12} < 0.01$, $p = 0.932$	UnCov $R^2 < 0.01$, $F_{1,12} < 0.01$, $p = 0.967$	UnCov $R^2 < 0.01$, $F_{1,12} = 0.11$, $p = 0.110$	UnCov $R^2 = 0.04$, $F_{1,12} = 0.56$, $p = 0.468$
	TotCov $R^2 = 0.02$, $F_{1,12} = 0.19$, $p = 0.674$	TotCov $R^2 = 0.06$, $F_{1,12} = 0.77$, $p = 0.398$	TotCov $R^2 < 0.01$, $F_{1,12} = 0.02$, $p = 0.889$	TotCov $R^2 = 0.09$, $F_{1,12} = 1.14$, $p = 0.307$
	FHD $R^2 = 0.05$, $F_{1,12} = 0.68$, $p = 0.426$	FHD $R^2 < 0.01$, $F_{1,12} < 0.01$, $p = 0.826$	FHD $R^2 = 0.09$, $F_{1,12} = 1.13$, $p = 0.309$	FHD $R^2 = 0.02$, $F_{1,12} = 0.24$, $p = 0.634$
	HH (-) $R^2 = \mathbf{0.29}$, $F_{1,12} = \mathbf{4.84^*}$, $p = 0.048$	HH $R^2 = 0.04$, $F_{1,12} = 0.47$, $p = 0.507$	HH (-) $R^2 = \mathbf{0.44}$, $F_{1,12} = \mathbf{9.47^*}$, $p = 0.010$	HH (-) $R^2 = \mathbf{0.49}$, $F_{1,12} = \mathbf{11.48^*}$, $p = 0.005$

Continued.

	Spring	Summer	Fall	Winter
Hawker density		Insufficient data	No data	No data
	Conifer $R^2 < 0.01$, $F_{1,12} < 0.01$, $p = 0.949$			
	Decid $R^2 < 0.01$, $F_{1,12} < 0.01$, $p = 0.948$			
	DBH $R^2 < 0.01$, $F_{1,12} = 0.96$, $p = 0.964$			
	TrDen $R^2 = 0.05$, $F_{1,12} = 0.66$, $p = 0.431$			
	ShDen $R^2 = 0.11$, $F_{1,12} = 0.13$, $p = 0.722$			
	ShSD $R^2 = 0.05$, $F_{1,12} = 0.67$, $p = 0.428$			
	UnCov $R^2 = 0.01$, $F_{1,12} = 0.07$, $p = 0.803$			
	TotCov $R^2 < 0.01$, $F_{1,12} = 0.01$, $p = 0.906$			
	FHD $R^2 = 0.01$, $F_{1,12} = 0.13$, $p = 0.725$			
	HH $R^2 = 0.01$, $F_{1,12} = 0.11$, $p = 0.745$			

Conifer: proportion of coniferous trees; Decid: proportion of deciduous broadleaved trees; DBH: mean dbh; TrDen: tree density; ShDen: shrub density; ShSD: shrub species diversity; UnCov: proportion of understorey foliage cover; TotCov: total foliage cover; FHD: foliage height diversity; HH: horizontal heterogeneity.
Insufficient data: more than five sites without data. No data: no records in that functional group in that season.
(+) positive relationship and (-) negative relationship, indicated only for relationships that are significant at $\alpha = 0.05$.
*Significant at $\alpha = 0.05$.