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**A MULTISCALE ANALYSIS OF NESTED SPECIES SUBSETS OF
FOREST BIRDS IN AGRICULTURAL LANDSCAPES NEAR
OTTAWA, CANADA**

By

Daniel G. Bert

A thesis submitted to
the Faculty of Graduate Studies and Research
in partial fulfillment of
the requirements for the degree of
Masters of Science

Department of Biology

Carleton University
Ottawa, Ontario
January 2001

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A MULTISCALE ANALYSIS OF NESTED SPECIES SUBSETS FOR FOREST
BIRDS IN AGRICULTURAL LANDSCAPES NEAR OTTAWA CANADA

Submitted by
Daniel G. Bert

In partial fulfillment of the requirements
for the degree of Masters of Science

Chair, Department of Biology

Thesis Co-Supervisor

Thesis Co-Supervisor

ABSTRACT

When species compositions for sites with low species richness are largely proper subsets of compositions for sites with higher species richness, the distributional pattern of species across sites is structurally nested. To date, the application of nested subset analysis has primarily focused on extensions of the theory of island biogeography, while largely ignoring spatial and landscape scale factors that potentially contribute to the generation of this class of non random pattern. In this study, two separate sampling designs were used to compare the effects of patch size, isolation, landscape structure and scale on species specific and assemblage level nestedness patterns. Standardized global and partial nestedness (species level) scores were calculated using a dataset comprising a total of 144 forest fragments with complete bird surveys in the form of presence/absence data in a 125 km² region near Ottawa, Canada, and representing a gradient of decreasing forest cover and increasing fragmentation. Nestedness varied greatly across ranking variables for both forest fragment zones and landscapes and increased with scale. Individual forest bird responses differed for landscapes ranked by independent measures of forest composition and configuration and also varied with scale. In general, only a small proportion of species was significantly nested. Because measurement error led to increases in statistical ties between sites for a given ranking variable, effect size and absolute nestedness scores declined with increasing error. Nested subset analysis may help identify species likely to exhibit threshold responses to landscape structure in a study region, which could lead to coarse scale rules for more detailed modeling in conservation management. However, researchers need to be aware that when comparing relative nestedness scores for different datasets, spatially explicit information including

scale, as well as estimates of measurement error on ranking variables and sampling and detection error for species lists, must be considered.

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June 21st 2000-First day of summer of the last year of the millenium...

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To Vanessa, thanks for every single day since all of this began.

There was once a lad so virtuous that the gods gave him a wish. His choice was to be, for a day, the charioteer of the Sun. Apollo was overruled when he predicted dire consequences, but subsequent events proved him right. The Sahara is said to be the track of desolation laid when the inexperienced driver let his carriage pass too close to Earth. Since then, the gods have tried to operate a closed shop.

M.N. Plano

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INTRODUCTION

Landscapes are being rapidly, and in some instances, irrevocably altered. As a result, the most pressing questions have shifted to how and where conservation efforts should be focused and to innovative ways to effectively transmit complex knowledge in a form that is easily understood and implemented by management agencies on the ground (White et al. 1997, 1999). The first step towards meeting either or both of these objectives is to appropriately describe the distribution of species in space and in time (Wright et al. 1998).

In the current state of conservation science, data are usually scarce, collected over short periods of time and usually at inappropriate scales to address conservation issues. In essence, scientists and managers are asked to find quick solutions to difficult questions with important and potentially long-term implications, across multiple scales using presence-absence species lists, and little else to guide further research.

Recently, nested subset analysis has taken on a prominent, albeit controversial role in this area of conservation research and in the general field of ecology. When species compositions for sites with low species richness are largely proper subsets of compositions for sites with higher species richness, the distributional pattern of species across sites is structurally nested (Patterson and Atmar 1986).

Alternatively, Wright and Reeves (1992) described nestedness through its relationship with the number of shared species across sites. When β diversity is lowest (similarity in species compositions is highest between sites), nestedness is highest and assemblages are non-random samples drawn from a common species pool in the same order (Wright and Reeves 1992). When beta diversity is highest (similarity is lowest)

nestedness is lowest and the species are sampled randomly (Coleman 1982). This definition makes a clearer connection between the nested pattern of species distributions and the implications of assemblage level structuring mechanisms to conservation: when nestedness is particularly strong, rare species will only be found in the most species-rich sites.

To date, research in this area has focused on three interrelated aspects of the nested subset pattern and the analysis of nested systems. First, several comparative and empirical studies have convincingly demonstrated that nestedness is a common feature of real islands and habitat fragments, across taxa and in wide ranging geographical contexts (Darlington 1957; Simberloff and Levin 1985; Patterson and Atmar 1986; Patterson 1990; Blake 1991; Bolger et al. 1991; Cutler 1991; Wright and Reeves 1992; Cook 1995; Kadmon 1995; Hecnar and M'Closkey 1997; Worthen et al. 1998; Wright et al. 1998; Calmé and Desrochers 1999; Fleishman and Murphy 1999).

Second, much debate and effort has been invested on developing an appropriate way to measure nestedness (Wright et al. 1998; Brualdi and Sanderson 1999). Several metrics have been proposed with each appearing to have both strengths and weaknesses depending on the application although no consensus has been reached (Patterson and Atmar 1986; Ryti and Gilpin 1987; Simberloff and Martin 1991; Cutler 1991; Wright and Reeves 1992; Atmar and Patterson 1993; Cutler 1994; Cook 1995; Lomolino 1996; Boeklen 1997; Brualdi and Sanderson 1999). Probably the most contentious issue to date has been the development of appropriate null models to evaluate the significance of observed patterns of nestedness (Simberloff and Martin 1991; Atmar and Patterson 1993; Cook and Quinn 1998; Wright et al. 1998; Brualdi and Sanderson 1999).

Elucidating the causal mechanisms behind the development of nested subset pattern has been particularly challenging and recent studies point to multiple causes interacting simultaneously to produce nestedness. Four hypotheses have been proposed for nested patterns of species distribution (Worthen 1996; Cook and Quinn 1998; Wright et al. 1998): (1) passive sampling, (2) selective extinction, (3) selective colonization and (4) habitat nestedness (Calmé and Desrochers 1999).

Passive sampling can produce a nested distributional pattern if common species have a higher probability of being sampled than rare ones (Coleman et al. 1982; Andrén 1994a; Worthen 1996; Worthen et al. 1998; Wright et al. 1998). The selective-extinction hypothesis (Patterson and Atmar 1986) assumes that species disappear from sites in a predictable sequence (Patterson 1990). In a forested landscape that has experienced a loss of habitat and an increase in fragmentation, for example, a strongly nested distribution pattern may indicate that a subset of species from the assemblage are area sensitive (Freemark and Collins 1992) and minimum area requirements or other critical area thresholds could be identified. According to the selective-colonization hypothesis, differences in dispersal ability will lead strong dispersers to occupy most sites whereas poor dispersers will be encountered only in sites where extinction rates are low (Cook and Quinn 1995). For those species with limited dispersal ability, isolation may lead to nested distributions at scales that match their respective response ranges and the nested distributional pattern could emerge directly or indirectly by influencing habitat choices. Several authors have argued that future studies should focus on the interaction between habitat and the development of nested distributions of species. If habitat composition and complexity is nested, then species responding strongly to key

habitat requirements will indirectly lead to a nested distributional pattern (Cutler 1994; Cook and Quinn 1995; Worthen 1996; Wright et al. 1998). To date, few studies have considered habitat explicitly in nested subset analysis (but see Calmé and Desrochers 1999).

Clearly, these hypotheses are not mutually exclusive and it appears likely that all can contribute and interact together, leading to the development of nested subsets. At the very least, nestedness is a complex distributional pattern that resists simple interpretation. Simberloff and Martin (1991) have suggested that this may limit its potential to inform conservation management strategies. To be a useful conservation tool nested subset pattern analysis must provide results that are easily comparable across scales, robust to measurement and sampling error of ranking variables and consistently identify species most strongly adhering to the hypothesis. Under these conditions, the causal mechanism driving nestedness is secondary.

Most studies have calculated nestedness with sites ranked by species richness while more recent studies have compared relative nestedness for sites ranked by area and isolation or by microhabitat richness (Cook 1995; Lomolino 1996; Calmé and Desrochers 1999). In this sense, nested subset analysis is an extension of applied island biogeography (MacArthur and Wilson 1967) and the analysis is essentially patch-centric. Most studies investigating the nested subset pattern have also focused primarily on a spatially implicit approach based on local scale variables while largely ignoring the landscape context in which the habitat fragments are embedded (Andren 1994a). Although forest fragment area has been documented as a major predictor of species richness, density and reproductive success for birds (Freemark et al. 1995; Bender et al.

1999). landscape scale factors have been shown to moderate forest area effects (Saunders et al. 1991; Freemark and Collins 1992; Fahrig and Merriam 1994; Robinson et al. 1995; Mazerolle and Villard 1999). Increasingly, the nature of the landscape surrounding a patch is also being recognized as important and that characterizing the effects of landscape structure on the persistence of populations is critical to conservation planning in the future (Whitcomb et al. 1981; Dunning et al. 1992; Freemark et al. 1995; Andrn 1997; Merriam 1998; Pope et al. 2000).

Recent work by Drolet et al. (1999), Trzcinski et al. (1999) and Villard et al. (1999) indicates that bird species respond differently to independent measures of habitat composition (type and/or amount of habitat) and configuration (spatial arrangement): combined these two components of spatial heterogeneity make up landscape structure (Fahrig 1998). Threshold responses to landscape structure are also predicted from theory (Fahrig 1997; Bevers and Flather 1999; With and King 1999). Extinction thresholds can be defined as the minimum amount of habitat below which the equilibrium population size is zero (Fahrig (in press)). For a given amount of habitat in the landscape, the principal influencing factors that determine the extinction threshold for a species are reproductive rate, rate of emigration from focal habitat patches, habitat configuration in the landscape and matrix quality (non-habitat areas) (Bascompte and Soul 1996; Fahrig 1997; Bevers and Flather 1999; With and King 1999; Fahrig (in press)). Relating nested pattern to landscape structure at multiple scales would be a major step forward in applying nested subset analysis to conservation efforts, while identifying species that are expected to exhibit threshold responses would greatly focus future research efforts.

In this study both patch and landscape scale sampling designs were used to study nestedness in birds in a fragmented, primarily agricultural region. Existing datasets comprising a total of 144 forest fragments with complete bird surveys in the form of presence/absence data were compiled for a 125 km² region near Ottawa, Canada, representing a gradient of decreasing forest cover and increasing fragmentation. Several independent sources of evidence indicate that birds and particularly Neotropical migrant species are at risk of extinction in at least a portion of their present range in southeastern Ontario (CWS 1998) and in many parts of North America, and the driving factor is thought to be large scale regional forest decline (Freemark and Merriam 1986; Wilson et al. 1986; Askins et al. 1987; Blake and Karr 1987; Robbins et al. 1989; Askins et al. 1990; Villard 1991). I calculated several patch and landscape scale metrics based on forested habitat. I used standardized metrics to calculate global and partial (species level) nestedness so that comparisons could be made between matrices differing in number of sites, species or both. Because of serious deficiencies in existing null models to test the significance of species x site matrices exhibiting a nested pattern of species distribution, a comparative analytical framework was adopted instead of a statistical one and using a neutral null model as a reference point. This approach has been recommended by Wright et al. (1998) and Cook and Quinn (1998) and this study currently represents the first application of this technique.

Study objectives were the following: 1) investigate the effects of area and isolation on nestedness in bird assemblages at the patch scale, 2) compare the relative effects of forest composition and configuration on nestedness at the landscape scale, 3) investigate the effect of ranking variable measurement error on nestedness, and 4)

determine if nested subset analysis has the potential to consistently identify species exhibiting threshold responses to structural characteristics of the landscape.

METHODS

Datasets

Three datasets collected between 1981 and 1990 (Freemark 1984; Villard 1991; Freemark and Collins 1992) were compiled. In total, 144 surveyed forest fragments were included in the study and fragments were largely clustered in six 10 km radius zones (Figure 1). Clusters were shared by fragments from different studies. Fragments sampled in more than one study were randomly assigned to one study dataset only and the remaining data from the other study(ies) for that forest fragment was/were not included.

As Villard (1991) indicates, only significant population trends throughout the study area could cause a bias due to the year of observation, which is unlikely for the set of bird species used in this study given their wide variety of migratory strategies and wintering ranges. I also wished to minimize variability in species distributions due to stochastic effects. Nestedness is a community level descriptor of species distributions (Worthen 1996) and I was more interested in comparing variable ranking strategies against the nested subset hypothesis and less so in year to year variation in species composition within forest fragment (turnover). Therefore, I pooled species assemblage data across years to establish the final presence-absence species x site matrix used in the analysis. While I concede that slight differences in design between studies may affect estimates of bird abundance, I believe that the presence or absence of a species was reasonably determined by each survey methodology.

Bird abundances were estimated using point counts, transects or both. Detailed descriptions of sampling and survey designs can be found in Freemark (1984), Freemark

and Merriam (1986), Freemark and Collins (1992), Villard (1991), Villard et al. (1995) and (1999). As recommended by Villard et al. (1999), I excluded all species that could not be detected efficiently by the survey methods (e.g., raptors and Ruby-throated hummingbird (*Archilochus colubris*)). Since rare and ubiquitous species can disproportionately affect nestedness scores and consequently bias results, species detected in fewer than 5% or more than 95% of forest fragment or landscapes (see design section below) were also excluded. I retained 71 species for further analysis including 14 “forest” bird species, as defined by Villard et al. 1999. All 71 species have ranges that coincided with the entire region of study, and therefore I assumed that each species had a finite probability of colonizing any single site or that all sites were colonized by a common regional species pool.

I followed the Villard et al. (1999) determination of bird species requiring forest for breeding.

Study Area

The original studies were conducted in a 125 km² region near Ottawa, Ontario Canada (45°25'N, 75°45'W), primarily in six 10 km² forested landscapes embedded in an agricultural setting along a gradient of decreasing forest cover and increasing fragmentation from north-west to south-east (Figure 1). The selection process for study sites set out to minimize within and among landscape variability of the structural and floristic composition of forest stands while maximizing variability in both landscape composition (forest cover) and configuration (fragmentation) between landscapes (Freemark and Merriam 1986; Villard 1991; Villard et al. 1995). Most remaining forest

fragments in the region are located on poorly drained soils of low agricultural value although some large forest tracts remain, including a provincial park (Gatineau park). Forest fragments in the region are relatively mature and dominated by sugar maple (*Acer saccharum*), white ash (*Fraxinus americana*), american basswood (*Tilia americana*), and ironwood (*Ostrya virginiana*), with occasional occurrences of eastern white pine (*Pinus strobus*) and eastern Hemlock (*Tsuga canadensis*). The region was approximately 36% forested as of 1992 (details below), a considerably higher proportion than that found in most nestedness studies on birds in agricultural contexts (e.g. Blake 1991).

Spatial data

For this analysis, I used 1992 National Topographic Database (NTDB) digital base map layers, which characterized forest cover to a resolution of 30 m. All other land- use classifications including agricultural areas were defined as matrix. Because of a persistent trend towards decreasing forest cover in the region, it is expected that 1992 maps will underestimate regional forest cover for the Freemark (1984) dataset and I considered this potential bias while interpreting the results. Maps were projected to UTM coordinates in a GIS using ArcView 3.2. I eliminated all forest fragments with areas less than 2.5 ha because they contained very little, if any core habitat.

Study design

I defined the 3 landscape sizes to study assemblage-level nestedness and individual species responses across scales. Traditional studies have used a patch-based

approach only. Forest fragment sites (islands or habitat patches) were differentiated by their contrast with the surrounding matrix (primarily agricultural). Based on their geographical proximity, I grouped the 144 fragments into 6 zones, or fragment clusters. I measured the percent forest cover in a circle of radius 10km roughly centered on each of the 6 forest fragment zones. Fragments falling outside of each zone were not considered in this part of the analysis but were included in the landscape scale design described below.

Following the design and recommendations of Villard et al. (1999) to study landscape effects and effects of spatial scale on the development of nested subsets in bird populations, I defined landscape sizes of 500, 1000 and 5000 ha. In contrast to Villard et al. (1999), I used overlaid hexagons instead of squares to define landscapes. Hexagons are generally considered to be superior to circles because they pack more efficiently, and to squares because they are probably more realistic from an organism's standpoint if the organism perceives the landscape equivalently in all directions. Hexagons (landscapes from this point on) were centered in such a way as to minimize occurrences of forest fragment intersecting hexagon boundaries. When fragments did intersect a hexagon boundary, I included it in the landscape that contained the greatest area of the fragment.

Species richness did not increase significantly when more than 2 fragments (regardless of size) were added in a landscape; therefore, landscapes containing at least 3 forest fragments were retained for further analysis, regardless of fragment size, and used to obtain an overall presence-absence of bird occupancy in a landscape. Based on these criteria, 40 (500 ha), 35 (1000 ha) and 20 (5000 ha) landscapes were retained for further

analysis. These scales should be appropriate for birds since breeding dispersal for most passerine species has been estimated at considerably less than 500 m (Villard 1991). In addition, Villard (1995) showed that fragment isolation on the order of several hundred meters was enough to significantly reduce the probability of fragment occupancy in several Neotropical migrants. Landscapes defined in Villard et al. (1999) were 625 ha in size. It is important to note that species probably respond individualistically to landscape structure at specific scales although the appropriate scales are usually unknown, and consequently the scales defined here are largely arbitrary and can only hope to capture average responses for most species.

I calculated a number of patch-based and landscape-scale metrics to use as ranking variables in the nested subset analysis. The nearest neighbor distance was defined as the closest edge-to-edge distance from a fragment exceeding 30 ha. I also used a buffer of 100 m to delineate core habitat and a buffer of 500 m for proximity index calculation (Gustafson and Parker 1994). Proximity buffers exceeding 500m gave qualitatively similar results. All spatial analysis was done using Patch Analyst, a spatial analytical extension designed for ArcView 3.x (Elkie et al. 1999; Rempel et al. 1999).

As recommended by Trzcinski et al. (1999), I calculated independent measures of forest cover (composition) and fragmentation (configuration) for the landscapes by conducting a correlation-based principal component analysis (PCA) of 6 variables: number of fragments (NP), mean fragment size (MPS), total core area (TCA), total landscape edge (TE), mean proximity index (MPI) and mean nearest neighbour (MNN).

Nestedness metrics

Several indices and approaches for quantifying nestedness in species-site lists have been proposed in the literature (Patterson and Atmar 1986; Ryti and Gilpin 1987; Cutler 1991; Wright and Reeves 1992; Atmar and Patterson 1993; Cook 1995; Lomolino 1996; Cook and Quinn 1998; Brualdi and Sanderson 1999) and as has been documented extensively, each metric appears to have both strengths and weaknesses. In this study the N_0 metric originally proposed by Patterson and Atmar (1986) was used. Following Wright and Reeves' (1992) notation, for a presence-absence matrix with **K** sites (rows) and **S** species (columns) with sites ranked by the absolute values of a variable of interest (e.g. area) where X_{ij} is the presence (1) or absence (0) for species *j* at site *i*. Species richness (row totals) is denoted by R_i .

$$N_0 = \sum_{i=1}^N \sum_{j=1}^{k-1} [1 - X_{ij}] \left[1 - \prod_{m=i+1}^k (1 - X_{mj}) \right]$$

For every entry $X_{ij} = 0$ and at least one $X_{mj} = 1$ in a site with a lower ranking variable score $m > i$ (e.g. species richness). For a species by site matrix ranked by species richness (generalized to any ranking variable), N_0 counts instances where a species is absent (0) from a site with higher species richness than the site with the lowest richness value on

which it does occur (1) and sums these instances for the entire matrix:

$$\begin{array}{c}
 \begin{array}{cccccc}
 s_1 & s_2 & s_3 & s_4 & s_5 & s_6 \\
 \begin{bmatrix}
 1 & 1 & 1 & 1 & 1 & 1 \\
 1 & 1 & 1 & 1 & 1 & 0 \\
 1 & 1 & 1 & 1 & 0 & 0 \\
 1 & 1 & 1 & 0 & 0 & 0 \\
 1 & 1 & 0 & 0 & 0 & 0 \\
 1 & 0 & 0 & 0 & 0 & 0
 \end{bmatrix}
 \begin{matrix}
 K_1 \\
 K_2 \\
 K_3 \\
 K_4 \\
 K_5 \\
 K_6
 \end{matrix}
 \end{array}
 &
 \begin{array}{c}
 \begin{array}{cccccc}
 s_1 & s_2 & s_3 & s_4 & s_5 & s_6 \\
 \begin{bmatrix}
 1 & 1 & 1 & 1 & \boxed{0} & 1 \\
 1 & 1 & \boxed{0} & 1 & 1 & \boxed{0} \\
 1 & \boxed{0} & 1 & 1 & \boxed{0} & 1 \\
 1 & 1 & 1 & \boxed{0} & \boxed{0} & 0 \\
 1 & 1 & 0 & 1 & \boxed{0} & 0 \\
 1 & 0 & 0 & 0 & 1 & 0
 \end{bmatrix}
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 \rightarrow
 \begin{array}{c}
 \begin{array}{cccccc}
 s_1 & s_2 & s_3 & s_4 & s_5 & s_6 \\
 \begin{bmatrix}
 1 & 1 & 1 & 1 & \boxed{0} & 1 \\
 1 & 1 & \boxed{0} & 1 & 1 & \boxed{0} \\
 1 & \boxed{0} & 1 & 1 & \boxed{0} & 1 \\
 1 & 1 & 1 & \boxed{0} & \boxed{0} & 0 \\
 1 & 1 & 0 & 1 & \boxed{0} & 0 \\
 1 & 0 & 0 & 0 & 1 & 0
 \end{bmatrix}
 \begin{matrix}
 K_1 \\
 K_2 \\
 K_3 \\
 K_4 \\
 K_5 \\
 K_6
 \end{matrix}
 \end{array}
 \end{array}
 \end{array}$$

Matrix A then represents a perfectly nested matrix and $N_0 = 0$. Empirical species-site matrices are rarely perfectly nested, resembling matrix B where $N_0 = 8$. Because N_0 is an absolute metric, scores are sensitive to matrix size. Under the equiprobable species null hypothesis, the analytical expected value of N_0 is:

$$E\{N_0\} = S \sum_{i=1}^k \left[1 - \left(\frac{R_i}{S} \right) \right] \left[1 - \prod_{m=1}^k \left(1 - \left(\frac{R_m}{S} \right) \right) \right]$$

The analytical equivalent to the Monte Carlo simulated RANDOM 0 (Patterson and Atmar 1986). $E\{N_0\}$ is the least constrained of class of null models used to test for departures from random matrices. Few common and rare species result from matrices produced under RANDOM 0 because each species is assigned an equal probability of occurring on any site. In other words, this model accounts for differences in row but not column totals.

A standardized form of the N_0 metric (PN_0) that allows comparisons between matrices of different sizes was proposed by Lomolino (1996) and also adopted by

Wright et al. (1998). PN_0 is reported as a percentage and varies between 0 and 100 with a score of 100 representing a perfectly nested matrix:

$$PN_0 = \left[\frac{(E\{N_0\} - N_0)}{E\{N_0\}} \right] \times 100$$

Another form that also controls for differential species incidences (N_{sa}):

$$N_{sa} = \frac{T}{(N_0 + T)}$$

where T is the total number of presences (1's) in the matrix (Cook 1995). This index is a relative measure of nestedness that is not affected by matrix size and varies from 0 to 1 (perfectly nested matrix).

To assess individual species contributions to nestedness, I used a standardized partial nestedness index. For any species j:

$$SN_j = N_{0j} / (\# \text{ absences})_j$$

This index effectively controls for differential occurrences of species in a distributional matrix (Calmé and Desrochers 1999) and also varies between 0 and 1.

While I am aware of its potential drawbacks (discussed in Brualdi and Sanderson 1999), I elected to use the standardized N_0 and N_{sa} metrics because 1) the metrics are easy to calculate, interpret and the frequent application of N_0 and standardized forms of the metric in the current literature provides us with a convenient reference point for my results (Cook and Quinn 1998; Wright and Reeves 1998), and 2) one of my objectives

was to study the effects of fragment and landscape descriptor variable rankings on nestedness and N_0 is sensitive to differential ranking orders of sites.

I agree with Cook and Quinn (1998) that RANDOM0 is currently the best alternative amongst a suite of models beset with potential biases and problems of estimating differences between species. Although a significant result between observed and expected scores under RANDOM0 does not allow us to test biologically relevant hypotheses regarding nestedness, it does provide an effective reference point for the objective of measuring relative effect sizes under different variable ranking constraints. I used Z values as an estimate of the difference between observed and expected values under the null hypothesis:

$$Z = \frac{\text{Observed}_{N_0} - E\{N_0\}}{\text{error}(\text{std.dev.})}$$

Error and ranked matrices

In this study, I am comparing relative nestedness scores under the equiprobable null hypothesis ranked by several variables $X_1, \dots, X_n$. By definition, when comparing the observed nestedness scores of matrices ranked by different variables, I assume that bias is effectively equal to 0 or at least that bias is *systematic* across all variables (which is unlikely). Here I use the Hellmann and Fowler (1999) definition stating that “*bias* is the difference between the expected value of the estimator (the mean of the estimates of all possible samples that can be taken from the population) and the true population value”.

When a nestedness metric is calculated, it is assumed that the observed nestedness value is an unbiased estimator of the true nestedness value. Secondly, site (row) rankings are based on *absolute* values of the variable in question, not magnitudes, and this potentially introduces another form of bias. For example, if the error $\mathcal{E}_i = \{S_i\} \cdot (X, p_i)$ on ranking variable $\mathbf{X}$ is equal to 2 and observations of variable $\mathbf{X}$ at sites K_1, K_2, K_3 , and K_4 are $\{4, 2, 20, 8\}$, the ranking order assigned to the matrix before calculating the nestedness score would be K_2, K_1, K_4, K_3 or K_1, K_2, K_4, K_3 because K_1 and K_2 are effectively tied. For error equal to or exceeding a value of 12 in this particular case, all sites would be considered equivalent and any ranking order would be valid. When error is included in the model, I ask the question “what is the distribution of true nestedness values given the observed value, and how does this affect results in general?”

All rank tests are based on the fundamental assumption that all the observed random variables are continuous, whereas in practice random variables $\mathbf{W}_1, \dots, \mathbf{W}_n$ are discrete and assumed to be independent with the same arbitrary, possibly discontinuous distribution function $\mathbf{F}$ (Hájek et al. 1999). Under these conditions, the ranks of tied observations are not defined and some modification of the test or metric is required. One of many proposed ways of dealing with ties is to employ some permutational method and then randomly draw one possible assignment from the distribution of possible permutations of the matrix with tied observations. The original algorithm of Patterson & Atmar (1986) did not explicitly account for ties in their N_0 metric, opting instead to randomly assign a rank to the rows (sites) with equal totals.

Wright and Reeves (1992) developed another method to account for tied observations (sites) in the calculation of observed and expected values of N_0 . For a ranked matrix under this scheme, observed N_0 gets incremented when the row total (for site K_i) is greater than the minimum species richness and does not when the row total for K_i is equal in richness (i.e. tied). From the definition of N_0 , all 0's that occur above a 1 for the focal site are counted. If a 0 is encountered above the focal site but the species richness (row total) is equal to that of the focal site, it is not counted in the N_0 score (Wright and Reeves 1992).

The procedure used for ties in the case of expected estimates of N_0 ($E\{N_0\}$ or Random0) is similar and involves a double sum over sites: i.e., for each focal site in a ranked matrix, if the row following the focal site has a richness value equal to that of the focal site, the contribution from that particular row is not taken into account in the calculation of nestedness. Here I generalize Wright and Reeves' algorithm for the observed and expected calculations to handle ties for any ranking variable.

Error estimates in fragment and landscape ranking variables

Because I wanted to study the range of possible effects of error on the ranking variables used in the nested subset analysis, I estimated error values based on a set of simplifying assumptions. For a given error rate of a variable E_p , I treated sites contained within the defined error bound in the same manner as numerical ties (see above section). The sole purpose of estimating error values in this case was to provide a reference point from which to establish an appropriate range for the error parameter.

I proceeded with the assumption that all errors were point-error estimates based on the resolution (30 m) of the digital maps I used to calculate the various patch and landscape scale indices that were used as ranking variables in the nestedness analysis. For any two randomly selected points A and B, the error on the distance D between the points is the square root of the sum of their respective variances $\sigma_{D(A,B)} = \sqrt{\sigma_A^2 + \sigma_B^2}$.

To simulate error on species richness for a set of sites, equivalent to the simplest case where species can be missed at any site with equal probability for an error range of 0- 20%, I generated a matrix of random numbers with cell values weighted by the error value in question. If the cell value in the random matrix was under the error value and the equivalent cell in the species x site matrix was of zero value (species absent at that site), the 0 (absence) became a 1 (presence).

Further details on the estimation of error for the variables used in the analysis can be found in Appendix 1.

RESULTS

Patch and landscape variables

Summary results for the various patch and landscape-scale variables in the 6 forest fragment zones (Figure 1) for 144 forest fragments are found in Tables 1 and 2. The distribution of forest cover in the 40 500-ha, 35 1000-ha and 20 5000-ha landscapes ranged between 5 and 70% (Figure 4) while other landscape-scale metrics varied considerably between landscapes (Table 2). Since landscapes in this study are defined as hexagons superimposed on the study region like a grid, 500 ha landscapes are nested within 1000 ha landscapes and 1000 ha landscapes are nested within 5000 ha landscapes.

Principal component analysis

For each of the three landscape sizes, the first principal component (PCA1) loaded highly on mean fragment size (MPS) and total core area (TCA) in each landscape at each scale. PCA1 scores were highly correlated with total area (TA) of forest in each landscape at all scales and was therefore equivalent to a measure of forest cover or composition. The second component, PCA2, by definition independent from PCA1, loaded most highly on number of fragments (NP) at all scales, and except at the 5000 ha landscape size, on total edge (TE) in the landscape and mean nearest neighbour distance (MNN). Therefore the second component was interpreted as an independent measure of landscape configuration.

Bird species

Incidences for all species in fragments and landscapes are indicated in Table 4. Species occurring in less than 10% of all fragments were not included in the analysis and do not appear in the table. Species occurring in less than 5 or more than 95% of fragments or landscapes for any part of the analysis were not included for that part of the analysis.

The distribution of species richness for the 144 forest fragments in the dataset was approximately normal (Figure 3) ranging from 2-43 species. Linear regression of $\log(\text{species richness})$ and $\log(\text{area})$ for the 144 forest fragments in the dataset (R^2 : 0.36, s.e. : 0.270, $p < 0.001$, $\alpha = 0.05$) was highly significant (Figure 5).

I investigated the dependence of species richness in a forest fragment zone on forest cover (Figure 6A) and the number of sites within a zone (Figure 6B) and found only weak relationships. The subset of 14 bird species that were most closely associated with the forest habitat that was characterized in the study (Villard et al. 1999) are highlighted in the Table 4.

Comparison of nestedness metrics

Cook's (1995) relative index of nestedness (N_{Sa}) is a metric that controls for differences in incidence between species. The N_{Sa} index accounts for differences in occurrence levels for different species. Since global nestedness for a set of sites (in this case forest fragments or landscapes) reflects species level differences in incidences, much of the variability in nestedness is controlled for with the N_{Sa} index (Wright and Reeves 1992). The apparent negative relationship between N_{Sa} and PN_0 with forest

cover (Figure 2) reflects this low sensitivity to a wide range of values in the ranking variable rather than the possible interpretation that both metrics are measuring different and opposite properties of the species-site matrices.

Although N_{Sa} does not accurately reflect the variability in nestedness between ranking variables, it can serve as a measure of residual variation related to factors external to differential species incidences. Because I was also interested in species level responses, I do not explore nestedness patterns with respect to the N_{Sa} metric any further here.

Patch-based design

Nestedness (PN_0) was higher for forest fragment zones than for all fragments combined, with the exception of zone 2. Zones represent subsets of forest fragments that share a spatial context (Figure 1). A clear trend along the gradient of increasing fragmentation and decreasing forest cover was not present. In general nestedness was higher when forest birds only were considered in the analysis (Figure 7B) although the difference amounts to less than 10%. Nestedness was strongest when forest fragments were ranked by species richness.

With the exception of zone 3 ($n=6$), matrices ranked by degree of isolation, as measured by the distance of a focal forest fragment to the nearest fragment equal or exceeding 30 ha, had the lowest nestedness scores and were consistently much lower than matrices ranked by fragment size (area or core area).

Partial nestedness scores can help identify the relative contribution of individual species to the overall nestedness pattern. Standardized partial scores can be compared to

determine which species are contributing, equally or disproportionately, to the overall assemblage level score. When species-site matrices are ranked by a variable of interest, the partial scores represent a measure of the predictability of the distribution of species across sites (in our case forest fragments or landscapes) with respect to the ranking variable. Because my index of partial nestedness is calculated as individual species contributions to the global nestedness score divided by the actual number of absences for any particular species (see methods section), a partial score for a species can be interpreted as the proportion of absences contributing to inflating N_0 and decreasing overall nestedness (PN_0 scores are lower). Consequently, comparatively low partial scores indicate a stronger adherence to the nested subset hypothesis for that species. To facilitate interpretation of partial nestedness, results are presented as $[1 - (N_0 / \text{\#absences})]$ (Figure 9). Higher partial scores indicate higher nestedness and no data values indicate a completely random distribution of the species across fragments when compared to the equiprobable null model. Similar to trends for assemblage level nestedness results, forest birds in zones had higher partial scores than those found when all fragments were considered (Figure 9). Partial scores were consistently higher for fragments ranked by species richness and lowest (often 0) for fragments ranked by isolation (nearest neighbour distance (NN)). With a few exceptions (Black and White Warbler, Yellow-bellied Sapsucker), species were more nested when ranked by core area (CA) rather than by area alone (A), especially in zone 5, and were often almost as nested as when species richness was used as the ranking variable. In general, partial scores were higher for zone 5.

Because my measure of partial nestedness is standardized, comparisons between species and across zones are valid. Forest bird species did not contribute equally to nestedness within and between forest fragment zones (Figure 9). For zone 2 (forest cover 36.3%), Hairy Woodpecker, Downy Woodpecker, Least Flycatcher and Veery were the most strongly nested species. Brown Creeper, Pileated Woodpecker and White-throated Sparrow were the most nested for zone 5 (forest cover 14.6%) (Figure 9). White-breasted Nuthatch had a completely random distribution for fragments in zone 2 whereas in zone 5, partial scores exceeded 0.3 for fragments ranked by species richness (SR) and core area (CA). Pileated Woodpecker was the only species to be perfectly nested for zone 5.

Landscape scale design

Landscape nestedness (PN_0) varied between ranking variables at all scales (different landscape sizes) and except for 500 ha landscapes was consistently higher for ranking by species richness (SR) (Figure 8). In general, nestedness was very low for 500 ha landscapes and increased with increasing landscape size; however, differences in nestedness were not as consistent across scale when matrices with all species were compared to matrices with forest birds only. While differences between 1000 ha and 5000 ha were marginal when all species were considered, differences were much stronger for forest birds at these two scales. This occurred through increased nestedness for 5000 ha landscapes and a decline in nestedness at 1000 ha, while 500 ha landscapes were only slightly higher (Figure 8) compared to matrices that considered all species.

PN_0 was generally higher for landscapes ranked by the measure of forest composition (PCA1) than for the measure of forest configuration (PCA2) (Figure 8). PCA1 increased and PCA2 decreased relatively as scale increased.

Because I wanted to compare nestedness for species across scales, we retained only the 13 forest bird species that occurred in more than 5% of landscapes for the species level analysis. With the exception of Pileated Woodpecker and White-throated Sparrow, which were more nested when 500 ha landscapes were ranked by the independent measure of forest composition (PCA1), most species showed higher nestedness when landscapes were ranked by species richness (SR) (Figure 10A). For many species, nestedness for landscapes ranked by PCA2 were highest for 1000 ha landscapes (Figure 10B). Similar to the assemblage level results, nestedness for sites ranked by forest composition (PCA1) increased relative to partial scores when sites were ranked by the measure of configuration (PCA2) as scale increased. At the 5000 ha landscape scale, several species (Ovenbird, Pileated Woodpecker, Veery) were perfectly nested when ranked by species richness (Figure 10C) while Scarlet Tanager was the only species to be perfectly nested with sites ranked by PCA1. Brown Creeper was also most nested with respect to PCA1 at the 5000 ha scale.

Species appeared to respond differentially within and across scales. For example, Hairy Woodpecker was completely random with respect to all ranking variables at the 5000 ha scale but was one of the most nested species at 1000 ha when sites were ranked by either species richness (SR) or PCA2.

Patch-scale/landscape-scale comparison

Although it is problematic to compare nestedness scores between the patch and landscape scale directly, we can make indirect statements about the influence of local compared to landscape scale on forest bird species nestedness patterns. When forest bird species were grouped by migratory strategy (grouped according to Freemark and Collins (1992)), average partial nestedness scores for fragments ranked by species richness followed the same trend as the partial scores for individual forest bird species (see Figure 9). However, resident birds did not follow the pattern, having much lower average partial nestedness scores for zone 2 (forest cover 36.3%) and much higher scores in zone 5 (forest cover 14.3%) compared to scores when all fragments were considered (Figure 11A). These results are similar to those described by Schoener and Schoener (1983) that indicated that migratory birds were more randomly distributed than resident birds on small Caribbean islands. These results differ from those described by Blake (1991) where nestedness for a set of forest fragments in Illinois was higher for the subset of Neotropical migrants than when all species were considered simultaneously. Forest cover in Blake's region of study was approximately 12%, similar to that found in zone 5. It should be noted that in both of these studies, nestedness was assessed for the subset of species included in a particular migratory strategy category and then compared to nestedness for all species considered together, whereas I used average partial nestedness scores for subsets in the matrix that included all species.

Conversely, resident species had almost identical average partial nestedness scores across all landscape sizes while both short distance and long distance

(Neotropical) migrants were much more strongly nested in the 5000 ha landscapes (Figure 11B).

Analysis of error

I measured the effect of ranking variable measurement error on nestedness (absolute Z) (Figures 12 and 13). Increasing error on ranking variables increases the number of sites that were considered tied statistically, effectively reducing the number of sites that contribute to nestedness. Responses to error varied considerably for both fragment and landscape scale variables but in all cases the effect was most pronounced for ranking variables with relatively high zero error nestedness scores and for small initial values in the range of possible error values. Error decreased estimated differences between observed and expected nestedness scores under the equiprobable null hypothesis. PN_0 decreased with increasing error for both fragments and landscapes across scales. I show only 1 example of each because results were qualitatively similar for different forest fragment zones and landscapes across scales.

The effect of error appears to be entirely dependent on the distribution of values for the ranking variable, the maximum range of the error parameter and the nestedness value when zero error is assumed.

DISCUSSION

Determining the relative influence of various causal factors that contribute to the commonly identified nested pattern of species distributions has been an elusive exercise. I provide evidence in this study that differential responses by bird species to landscape structure and scale may also influence the assembly of ordered species compositions. For this study region at the patch scale, nestedness was highest for forest birds in forest fragment zones with low forest cover and relatively high fragmentation. Fragments sorted by area were by far more nested relative to sites ranked by isolation. At the landscape scale, nestedness increased with scale, as did landscapes ranked by independent measures of forest composition relative to landscapes ranked by forest configuration. Few species were drivers for the nested subset pattern although different sets of species were most strongly nested depending on the study design (patch vs. landscape) or the ranking variable. Of the forest bird species studied, resident species were highly nested compared to migratory species in landscapes with low forest cover and high fragmentation, whereas Neotropical and short-distance migrants were most nested in the largest landscape sizes studied. As far as I am aware, this study represents the first example of a multiscale analysis of nestedness and at this stage it should be considered as an exploratory investigation.

Overall bird nestedness is relatively low for this study region compared to other published results, although the values are still well within the range reported in other studies (Blake 1991; Cook 1995; Wright and Reeves 1992; Cook and Quinn 1998; Wright et al. 1998). Regional forest cover is still relatively high in southeastern Ontario and although regional declines in bird species have been detected, these decreases may

not have reached critical threshold levels for many species that could lead to local extirpation in a set of fragments (Fahrig 1997). However, differential nestedness scores between forest fragment zones along a gradient of decreasing forest with a common regional species pool indicates that bird assemblages in areas with high forest cover at the time of the study could resemble assemblages found in areas with the lowest forest cover if current trends in the rate of land conversion persist or accelerate in future. Although total species richness may not differ significantly between areas of low and high proportions of suitable habitat, a different set of species are likely to predominate given a regional pool of species with finite probabilities of colonizing any particular site in question. Describing nestedness as a common feature of ecological assemblages. Gotelli and Graves (1996) suggested that researchers should focus on species that deviate from nestedness instead of the majority that adhere to the pattern. Our results indicate that most species do not conform to the nested subset hypothesis and therefore our focus will instead be aimed at species that show evidence of having a nested distribution.

Patch-based analysis

Our patch-based design investigated nested subset patterns as a simple extension of the theory of island biogeography (MacArthur and Wilson 1967) applied to habitat islands, in this case forest fragments embedded in a matrix primarily composed of agricultural fields and suburban development. The result that assemblage composition is more predictable for sites ranked by area rather than by isolation is consistent with results found by Lomolino (1996). Given that a systematic analysis of the behavior of

nestedness metrics has yet to be completed, comparing results from different metrics directly may be problematic.

Standardized nestedness values (PN_0 from this point) were higher for forest fragment zones than when all fragments were considered together (Figure 7). Nestedness was also greater when forest bird species were considered alone. Nestedness is expected to increase with increasing similarity of assemblages between sites, and consequently, decreasing β . This effect follows from the expectation that sites with similar species richness that are highly nested will have highly similar species compositions as well. Consequently, the degree of nestedness for a set of sites is correlated with the average similarity in species compositions among sites (Wright and Reeves 1992; Gotelli and Graves 1996). These conditions should be most pronounced in areas with the lowest forest cover (and highest fragmentation) where it is expected that many species have been lost in forest fragments that are either too small or isolated. It also follows that significant spatial autocorrelation will also increase nestedness for the same reasons previously described (see future directions section below).

PN_0 scores varied little between zones with highly contrasting proportions of forest cover, suggesting that factors within a zone other than the proportion of suitable habitat may have a larger influence on species distributions. The ordering strategy for sites within a zone had little effect on the PN_0 score as well although sites ranked by species richness usually adhered most strongly to the nested subset hypothesis. Our study supports results from other studies that found that sites ranked by species richness were often more nested than when sites were ranked by area (Cook 1995; Wright et al. 1998; Calmé and Desrochers 1999).

For the species-level or partial nestedness analysis, I focused on forest bird species only since the patch and landscape scale variables characterized forested habitat only and considered all other land use classes as non-forest. Partial scores for forest bird species could be interpreted as the proportion of absences in the matrix contributing to the global nestedness score. Partial scores were standardized for differences in species occurrence allowing for meaningful comparisons (see methods section). Few species contributed strongly to nestedness (Figure 9). For the patch-based design, species responded very little when all fragments were considered simultaneously and more strongly for individual zones but nestedness differed between zones with highly contrasting proportions of forest cover. Nestedness based on different ranking variables paralleled that found for assemblages (figure 7). This demonstrates that species differentially contributed to the nestedness score for a set of fragments. The species that seemed to drive the nested subset pattern (ex. Pileated Woodpecker) were those that require forest interior habitats (Freemark and Collins 1992).

It is possible that the ranking variables I have used in this study do not accurately resolve spatial differences in species distributional patterns. For example, in all cases, sites ranked by the distance to the nearest fragment exceeding 30 ha, a presumed pool of potential colonists showed very little nestedness relative to fragments ranked by area, consistent with Wright and Reeves (1992). Zone 3 (see Figure 1) was an exception to these trends. This may be simply an artifact related to the number of sites ($n=6$) which was much lower than for other zones. Despite using standardized metrics that are insensitive to matrix size, Wright and Reeves (1992) noted that matrices with few sites tended to show unstable nestedness scores.

These results seem to indicate that differential colonization abilities play little role in the development of nestedness in birds in forest fragments in this study region and supports the extinction driven nested subset hypothesis (Patterson and Atmar 1986). The strongest evidence for the extinction hypothesis comes from the pattern of nestedness observed in zone 5 (forest cover 14.3%) for individual species (Figure 9C). In zone 5, nestedness for most species is stronger for core area than area alone. The same pattern exists in zone 2 but it is much stronger in zone 5. When habitat becomes highly fragmented, often very little core habitat remains because small remnant fragments replace larger continuous tracts. If core habitat is a limiting factor for several bird species, then those bird species should be highly nested with respect to core area, which fits the observed pattern. Yet, even under these conditions, nestedness with respect to isolation is very low and much lower relative to nestedness ranked by either area or core area.

In the only other study to investigate the relative effects of colonization and extinction using an analysis similar to the one used here, Lomolino (1996) found that sites ranked by area and isolation were equally nested for nonvolant mammals and in many cases isolation was a stronger ordering factor. Breeding dispersal for most passerine species has been estimated at considerably less than 500 m (Villard 1991) and Villard (1995) showed that fragment isolation in this study area on the order of several hundred meters was enough to significantly reduce the probability of fragment occupancy in several Neotropical migrant species. Villard et al. (1995) suggested that site fidelity might be an important constraint on the distributional dynamics of these species, even when effects of fragment area and habitat on site fidelity are factored out.

In both of these cases, isolation would be expected to represent a strong ordering force for the development of nestedness.

Low nestedness for fragments ranked by isolation does not preclude colonization from being an important causal factor in the distribution of species in forest fragments in agricultural landscapes. It does indicate that the relative contribution of colonization is probably much weaker than that of extinction. Analysis of nestedness for forest birds grouped by migratory status provides support. Resident birds were 3 times more nested in zone 5 (forest cover 14%) compared to zone 3 (forest cover 36%). In contrast, Neotropical and short-distance migrants showed very little difference in average nestedness across zones (Figure 11A). This was not the case for the landscape nested subset analysis (see below). Blake (1991) reported higher nestedness for Neotropical migrants than for resident birds when these subsets were analyzed separately. The study was conducted in Illinois where regional forest cover has been reduced to less than 11%. Blake (1991) considered all forest fragments together in his analysis; in other words, nestedness was not measured for fragments in contrasting landscape contexts like it was here. Taken together, I suggest that threshold responses for most forest bird species have yet to be reached for this region. Resident species do not select habitat upon returning from wintering grounds like migratory species do each year. As a result, they are expected to experience negative effects from habitat loss and fragmentation first since they are more restricted in their scale of movement (Merriam 1988; Merriam 1998). Still, resident birds are strongly nested only in landscapes with very low forest cover (ex. zone 5). While this region of study has experienced habitat loss and fragmentation for over 100 years (Villard 1991), the rate of change due to rapid

conversion of forested lands to suburban development in the past 20 years is unprecedented. Those bird species that were too rare to be included in this analysis may have already exceeded threshold levels of habitat loss.

It should be noted that it is also likely that my measure of isolation (nearest neighbor distance) is either inaccurate or does not adequately reflect the range of respective species-specific perception of isolation (see landscape scale analysis for metric limitations) (Lomolino 1996; Bender et al. (unpublished)).

Landscape scale analysis

In general, nestedness for landscapes for all ranking variables increased with landscape size. Variability between ranking variables was low, including the independent measures of forest composition (cover) and configuration (fragmentation) (PCA1 and PCA2, respectively) (Figure 8). Nestedness for landscapes ranked by PCA1 increased relative to landscapes ranked by PCA2 with increasing scale. A fundamental property of fractal landscapes is that landscapes of larger extent contain larger patch sizes (Milne 1992). As a result, the number of possible configurations (variability) for larger forest fragments decreases as scale increases, or in this case, as the extent of the landscape increases (Bert unpublished). The independent measures of forest composition and configuration are based on metrics that we assume appropriately characterize landscape structure. We further assume that the underlying metrics capture the range of structural differences across landscapes (Hargis et al. 1998).

Partial scores were much more variable (Figure 10). For the landscapes, species appear to have responded at specific scales with many species responding only at one

scale. Almost all species responded to the measure of forest composition in certain landscape subsets at certain scales, and to forest configuration in others. In other words, the set of species adhering strongly to the nested subset hypothesis differed when sites were ranked by composition or configuration. This supports the hypothesis that bird species probably respond individualistically to landscape structure at specific scales (Mazerolle and Villard 1999), although the appropriate scales are usually unknown, and consequently the scales defined here are largely arbitrary and can only hope to capture average responses for most species (but see Wiegand et al. 1999).

In general, forest birds appear to be most strongly nested as a group with respect to forest composition (PCA1, forest cover), although different sets of species were identified for composition and configuration components (Figure 10). These results support those found by McGarigal and McComb (1995), Trzcinski et al. (1999) and Drolet et al. (1999) that forest cover and not configuration is the most important predictor of bird presence or absence and abundance. It must be noted that in none of these studies was it suggested that configuration was not an important factor. In contrast, Villard et al. (1999) indicated that both composition and configuration were important.

However, each study was conducted at a single scale. Landscapes of approximately 900 ha studied in Oregon by McGarigal and McComb (1995) were embedded in relatively continuous mature forests. Drolet et al. (1999) studied forest birds in small (100 ha) clearcut landscapes in Quebec boreal forest. Trzcinski et al. (1999) used 10 000 ha landscape grids in Eastern Ontario agricultural landscapes, as did Villard et al (1999) using 625 ha landscapes. The scales studied here (500, 1000, and

5000 ha) overlap all but the largest of the four designs outlined previously. Both McGarigal and McComb (1995) and Drolet et al. (1999) argued that landscape context, historical natural disturbance patterns and the rate of regrowth of clearcuts may have led to a low effect of configuration. In other words, they contend that regardless of the scale of investigation, composition effects would dominate. It is also possible in these studies that the scale of investigation defined *a priori* precluded the investigators from detecting equally strong signals of composition and configuration. For example, when forest birds were grouped by migratory strategy, average partial scores were much higher in 5000 ha landscapes for Neotropical and short distance migrants whereas resident species showed very little variability across landscape sizes (Figure 11B). As previously discussed the relative contribution of composition to landscape structure increases compared to configuration with increasing scale. At the local scale, resident birds were more strongly nested than migrants (see patch-based design section) indicating that the characteristic scale for this group as evidenced by adherence to the nested subset hypothesis at the patch scale, is considerably lower than the 500 ha landscapes I have defined here.

It also follows from this argument that the probability of detecting configuration effects decreases with increasing scale. Studies at large scales such as Trzcinski et al. (1999) may fall into this category where effects of composition are more likely to be detected and configuration effects, if present, are masked for most species. My results indicate that configuration effects are more likely to be detected at small scales for species that have relatively limited dispersal ability. The question that is often asked is 'for a certain group of species, is composition more important than configuration?'

Perhaps the appropriate question should be 'at this particular scale, is composition more important than configuration for this particular species?' Evidence from Villard et al. 1999 indicates that at least for forest birds, composition and configuration are equally important at the scale of analysis used in the study (625 ha landscapes).

The scale of heterogeneity should be based primarily on the perception of the organism studied (Wiens and Milne, 1989; Goodwin and Fahrig 1998; Mazerolle and Villard 1999; Wiegand *et al.* 1999). If different species perceive heterogeneity in the environment at different scales then it may not be appropriate to measure environmental variables or population responses at the same scale for all species. Whereas my results have shown that many bird species are more highly nested at specific scales and for key components of landscape structure, the 3 landscape sizes defined here are probably adequate for capturing average dispersal distances for most species in the dataset (Villard 1991). A threshold value of habitat of about 20% is predicted (Andrn 1994b; Fahrig 1997; Fahrig (in press)), below which effects of habitat fragmentation on population persistence may exist. Villard et al. (1999) suggested that for a given amount of habitat, configuration effects could explain patterns of occurrence for different species. I predict that in many studies thresholds are not detected because the scale of investigation does not match the scale of movement of the organism. Nested subset analysis can inform investigators about which species are expected to show threshold responses to landscape structure.

Effect of error on nestedness

The effect of error on nestedness measured was very consistent across patch and landscape based variables. For both fragments and landscapes increasing error led to a decrease in effect size ($|Z|$) and a decrease in PN_0 . Increased error led to an increase in the disorder of the observed matrix, a consequent decrease in effect size between observed and expected nestedness under the equiprobable null hypothesis and a decrease in PN_0 . The only factors that seem to influence the relationship between error and effect size are the range and distribution of absolute values of the variable in question and the nestedness score at zero error.

I simulated error on matrix species richness per fragment or landscape (incomplete species lists) by randomly assigning a number to each species x site cell in the matrix. If that cell value was equal to 0 (absent) and the assigned number was lower than the error value (for that step size), the 0 was changed to a 1. Because all species and sites had equal probabilities of being 'switched', and because I did not attempt to weight the matrix by the species that would be most likely to remain undetected or for differential sampling intensity across sites, this is the simplest model I could have used to simulate this process (Boulinier et al. 1998).

I did not consider the possible effects of error in species lists caused by factors external to the observer. If the probability of detecting a certain species, given that it is present, is independent of the size of the sampled fragment or the proportion of forest cover in the landscape (for example), then sampling is unbiased with respect to these variables. Therefore, the estimates of nestedness will also be unbiased if this holds true for all species and the rank order of sites would be stable. On the other hand, if

sampling is biased, such that the probability of detecting a species, given that it is indeed present, does depend on the size of the sampled forest fragment or the proportion of forest cover in the landscape (which is almost certainly the case), then our estimate of nestedness will be biased. However, if the probability of detection is biased systematically for all species in the regional pool, then our results will be qualitatively similar and our estimate of nestedness would not change since the rank order of sites would still be stable. Thus effects external to observer error (missing a species that is in fact present) that can alter species lists may exacerbate sampling bias and could result in spurious nestedness scores, especially if the inherent bias changes across landscapes.

Another factor that I did not explicitly investigate in this study relates to species missed at all sites. For regionally rare species, there is a finite probability that those species will be missed at all sites and matrix size is underestimated. Gotelli (2000) investigated of what he called 'degenerate matrices' and found that under certain circumstances these could influence whether or not the null hypothesis was rejected. Because I eliminated all species occurring in less than 5% of forest fragments or landscapes, I expect that this problem is at least partially mitigated. However, it should be noted that for many taxa and especially in birds, low levels of occurrence are commonplace. This is yet another reason that the accuracy of species lists should be carefully assessed before analysis begins.

I do not expect that measurement error or error based on differences in the probability of detection in sampling designs to be systematic between studies and across taxa. Therefore, the distribution and range of a ranking variable is a critical element in estimating the effects of error on nestedness scores. For example, it is very common in

bird studies to have a fragment size distribution that is left skewed. In this case, if measurement error on the estimation of fragment size is small overall but large relative to the small fragments, then the effect of error on nestedness will not be spread uniformly across the entire distribution of fragments sampled in the study. In other words, there will be a bias towards small fragment sizes and the resolution of absolute site rankings for the smaller fragments will be undefined for those sites. The larger the matrix and the more continuous the values of a given variable, the slower the decline in effect size (and PN_0) with increasing error. If species are responding to some ranking variable, the greater the range in that variable and the greater the difference between values of the variable, the more I expect nestedness to develop (Wright and Reeves 1992; Wright et al. 1998). Strongly nested systems will therefore be most affected by measurement or sampling error and since at least some error can usually be assumed, most published nestedness values based on existing metrics are overestimated.

Another area of concern is that in general, the number of landscapes is low compared to the number of forest fragments (Table 2 and 3) and with it so is power. Further, smaller landscapes (500 and 1000 ha) are nested within larger landscapes (5000 ha). While a focal patch approach of defining landscapes would have increased the number of landscapes at all scales, most fragments are clustered and using this method would result in overlapping landscapes that would lead to a lack of independence (Brennan et al. (in press)). I calculated nestedness within a landscape size only and this should adequately control for any potential issues of non-independence.

Analytical framework for nested subset analysis

These results suggest that nestedness scores from all habitat fragments or landscapes (forested habitat in this study) in a region could be used as a comparative baseline reference or signal. Figure 14 illustrates an application of the technique for forest fragment zones 2 and 5 (proportion of forest cover 36 and 15%, respectively). The difference between nestedness for a focal landscape (in our case zones 2 and 5) and the background value has been calculated. The result can be interpreted as a relative measure of nestedness for each species using nestedness values for those species at the regional scale as a reference point. With this type of analysis, it is possible to begin to answer the following question: with respect to some ranking variable, is this species more or less nested than it is in the regional pool when all sites are considered (in this case forest fragments in zones)? Of the 14 forest bird species, 8 are more nested compared to reference in the landscape with the lowest proportion of forest cover (zone 5), 4 are less nested and some show very little difference. If a landscape (zone 2 and 5) can be considered as an assembly 'filter' (Weiher and Keddy 1995; Weiher et al. 1998), the response of each species compared to background is an indicator of the strength of the filter with respect to a ranking variable of interest for that species. The landscape filter in this case is overall habitat availability (forest cover). Species that do not have large differences (positive or negative) in scores compared to background in any of the landscape contexts studied (in our case zones) will not exhibit threshold responses with respect to the ranking variable in question.

Further analysis in specific locations of interest using nestedness scores for sites or landscapes ranked by species richness could be used as a measure of maximum

possible nestedness. Both of these measures could be combined to produce a relative measure of regional nestedness for a particular group of species. Ultimately, acceptable null models and appropriate metrics capable of accurately characterizing the degree of nestedness and assessing the significance of a particular metric score will be required. Future studies must incorporate these potentially important factors explicitly as part of their analysis. Research on the behavior of current and possible new metrics that quantify nestedness and their sensitivity to error under a variety of conditions (probably through simulation) is required to provide an appropriate framework for comparison of nestedness scores, or preferably, relative effect sizes to enable cross regional comparisons for conservation management of species across large portions of their geographical range.

Future directions

In previous sections I have alluded to several technical issues that have superseded practical advances in nested subset theory and use of the analysis as a tool for conservation management. Central to these concerns is the construction of appropriate null models (Sanderson et al. 1998; Brualdi and Sanderson 1999). Null models proposed by Connor and Simberloff (1979) to test for competition effects in species co-occurrence matrices began an incredible run of critical work from Diamond and Gilpin (1982), Gilpin and Diamond (1982), Connor and Simberloff (1983), and Gilpin and Diamond (1984). The use of null models in ecology was and is contentious (Diamond and Gilpin 1982; Roughgarden 1983; Simberloff 1983; Wilson 1987; Roberts and Stone 1990, Stone and Roberts 1990, 1992). Putman (1994) remarked that the

debate was “almost unprecedented in the apparent entrenchment and hostility of the opposing camps”. Null models used in the study of nested subsets has also received much attention because null model methodology is applied here also (Patterson and Atmar 1986; Cook 1995; Cook and Quinn 1995; Simberloff and Martin 1991; Sanderson et al. 1998; Wright et al. 1998; Brualdi and Sanderson 1999). The debate rages on and is far from being resolved. An excellent review on the history of the null model debate can be found in Gotelli and Graves (1996).

Determining whether or not a species assemblage is structured randomly is dependent on the choice of sample space. Much of the controversy related to null model analysis has centered on defining the appropriate ‘null’ sample space (Connor and Simberloff 1979, 1983, 1984; Diamond and Gilpin 1982; Gilpin and Diamond 1982). Most randomizations fix rows, columns or both (Patterson and Atmar 1986; Connor and Simberloff 1979; Simberloff and Martin 1991; Sanderson et al 1998). Brualdi and Sanderson (1999) assert that fixing row and column totals should generate the appropriate ‘null’ sample space. I disagree primarily because this method constrains the sample space to a subset of matrices that match the distribution of species found in the observed data exactly. Many researchers agree (reviewed in Gotelli and Graves (1996)). As a result, I adopted a comparative analytical framework instead of a statistical one and used a neutral null model as a reference point. This approach has been recommended by Wright et al. (1998) and Cook and Quinn (1998) and while it is clearly not an ideal strategy because it falsely assumes that all sites and all species are equivalent, it may represent the best possible alternative at present.

I do agree with Brualdi and Sanderson (1999) that metrics used to estimate nestedness must be improved. Currently, nestedness values are often calculated using the Patterson and Atmar (1986) methodology that counts absences (0's in the ranked presence-absence matrix) that do not conform to the nested subset hypothesis (see methods section for details). The perceived problem for using this methodology is that counting "gaps" tends to be biased towards an extinction-driven cause for the development of nested subsets (Brualdi and Sanderson 1999). Another issue that has received much less attention is that current metrics are not fully characterized. No sensitivity analysis or systematic assessment of metric performance under a wide range of conditions has yet been completed (Wright and Reeves 1992; Wright et al. 1998). Consequently, we have only a very crude understanding of what constitutes high and low levels of nestedness for a particular ranking variable in a particular landscape context. Despite the theoretical and practical importance of expanding our understanding of null model and metric behavior, my results here indicate that the effect of error can be at least as great in assessing the significance of any distributional pattern that depends on site rankings for metric calculation. It is my belief that determining reasonable error bounds for any particular region will be difficult and in some cases impossible and may represent the single most important challenge to wider acceptance and applicability of nested subset analysis. Because a comparison of responses for species in contrasting landscape and regional contexts is central to resolving issues related to identifying future conservation targets, this area of study will require further attention and development.

Wright and Reeves (1992) suggested that nested subset analysis could be used as a statistical clustering technique at the assemblage level. As previously discussed, this largely follows from the property that the degree of nestedness for a set of sites is correlated with the average similarity in species compositions among sites (Wright and Reeves 1992; Gotelli and Graves 1996). In this study, spatially clustered forest fragments (zones) were more nested than when all fragments were considered simultaneously. I used spatially explicit measures of landscape structure as ranking variables in the nested subset analysis, but I still have not characterized how nestedness varies through space (for my study region) and with scale (or given appropriate data with time as well) and under which set of these factors is nestedness maximized. Since in one sense nestedness is a measure of β diversity, it could be used as a metric of similarity in an analysis of spatial autocorrelation to study the pattern of nestedness in space. A working hypothesis is that positive spatial autocorrelation of a ranking variable of interest should increase nestedness because sites that are in closer spatial proximity will exhibit a higher propensity to be statistically 'tied'. The same principal applies if a matrix is ranked by species richness: the prediction under positive spatial autocorrelation is that sites in closer proximity will share more species. In other words, at least part of the nested subset pattern could be explained by a lack of independence in sampling sites. This appears to be a broad and rich area for further research.

Conservation implications

Interest in nested subsets as a distributional pattern has largely revolved around its potential to inform decision making in reserve design; as a result, nested subset analysis has been irrevocably linked to and at times embroiled in the SLOSS debate (single large or several small reserves) (Patterson and Atmar 1986; Cutler 1991; Simberloff and Martin 1991; Cutler 1994; Cook 1995; Kadmon 1995; Boeklen 1997; Cook and Quinn 1998; Fleishman and Murphy 1999). In a perfectly nested matrix, it is possible to predict the sequence of occurrences for each species in an assemblage for a set of sites under investigation. If sites are ranked by species richness or by the size of the site, strong nestedness implies that large reserves are needed to conserve the rarest species. Inferences to this affect are simply extensions of the theory of island biogeography that also include species composition as part of the framework. As nestedness declines, the predictability of species occurrences at the assemblage level also decreases and assemblage composition becomes more variable. In this case, the connection between reserve size and nested subsets is less clear, leaving some authors to doubt the significance or practical implications of nested subsets for conservation (Boeklen 1997; Whittaker 1998).

Several other lines of study suggest that nested subset analysis may have potential applications beyond the SLOSS debate. Increasing evidence suggests that nestedness is stronger in landscapes that have experienced habitat loss and fragmentation to such an extent that thresholds have been reached or exceeded (Blake 1991, this study). My study also suggests that even when nestedness is low at the regional scale, key areas and species that drive the nestedness pattern can be identified

readily with the technique at the patch scale. Finally, I have shown here that species compositions at the landscape

scale are also nested with respect to structural characteristics of forested habitat. Increasingly there is a need for conservation tools that can be applied to existing datasets with a minimal set of assumptions. Nested subset analysis appears to hold promise in serving this function as well.

Understanding the impacts of habitat loss and fragmentation on biodiversity and predicting impacts related to future landscape change has become a central focus of conservation ecology (Heywood and Watson 1995; Chapin et al. 1997). Growing rates of destruction in recent decades underscore the need for development of spatially explicit models that consider multiple species across taxa and distribution ranges, landscapes, and regions to help guide management strategies faced with alternative landscape change scenarios (Hansen et al. 1995; Freemark et al. 1996; White et al. 1997). Models that incorporate local information on community structure and dynamics at fine spatial scales will improve the identification and assessment of risks posed to biodiversity at landscape and regional scales, where policy initiatives are usually implemented (Freemark 1995; White et al. 1997).

The interesting result that different species appear to drive the nested pattern when different study designs are adopted may provide the strongest evidence that landscape context is related to assemblage level structuring in birds, at least for some species. Nested subset analysis may be used as a precursor to other types of analysis to help identify the characteristic scale at which individual species are expected to respond.

The relationship between the characteristic scale of response for each of the forest bird species, their adherence to the nested subset hypothesis and their relative propensity to exhibit threshold responses to landscape structure is not entirely clear. Our analytical framework does not permit us to make specific inferences regarding the relative strengths of individual responses to landscape structure. Still, some species did not contribute to nestedness for most ranking variable and some species only responded at specific scales (ex. Veery). It may be possible to differentiate in a binary fashion species that might be expected to show threshold responses to landscape structure. These species were those with partial nested scores greater than 0 at any particular scale (Figure 10). Simple rules such as these can be helpful in future modeling work.

This study represents a first step towards developing a multi-species, spatially explicit set of rules for conservation and risk assessment with respect to bird communities across regions in North American agricultural landscapes. If predictable patterns of nestedness exist for multiple species across regions, these standards could be incorporated into models that assess risks posed by future landscape change scenarios.

CONCLUSION

While nested subset analysis appears to identify areas that are particularly nested and species that adhere strongly to the nested subset hypothesis, I suggest that potential error biases in species lists and on ranking variables as well as the impact of scale on nestedness make absolute comparisons of standardized nestedness values between studies and across taxa problematic. However, it is precisely this sensitivity to patch characteristics, landscape structure and scale that increases the potential of nested subset analysis to inform conservation decisions by identifying key species that are expected to exhibit threshold responses. Instead of attempting to find conclusive evidence that the pattern does in fact exist, further research should focus on developing an analytical framework for nested subset analysis that better serves these objectives.

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APPENDIX I

I proceeded with the assumption that all errors are point error estimates based on the resolution of the digital maps I used to calculate the various landscape indices (ie. 30m). I assumed in each case that all variables have independent random errors and a common systematic error. For any two randomly selected points, A and B, the error on the distance D between the points is the square root of the sum of their respective variances:

$$\sigma_{D(A,B)} = \sqrt{\sigma_A^2 + \sigma_B^2} \quad \text{Eq. 1}$$

The general case for error estimation for a 2 parameter variable:

$$Z = f(x, y) = \sigma_Z^2 = \sqrt{\left(\frac{\partial z}{\partial x} \cdot \sigma_x\right)^2 + \left(\frac{\partial z}{\partial y} \cdot \sigma_y\right)^2 + 2 \text{cov}(x, y) \frac{\partial f \partial f}{\partial x \partial y}} \quad \text{Eq. 2}$$

The landscape metrics measured in this study are primarily based on average values (e.g. mean fragment size) and since I do not have an underlying distribution for these values, the covariance term is unknown. Estimating it as $\sigma_x \sigma_y$ will give a perfect correlation between variables. Therefore, it was assumed that the variables are independent, in which case the covariance term above is identically zero.

This will not affect the calculation of the nestedness metrics, regardless of the ranking variable used, since the error estimates themselves are not used in any calculation. Their sole purpose is to provide a reference point from which to establish an appropriate range for the error parameter.

I assumed that the area of all forest fragments (and core area) could be estimated by the area of a circle

$A = \pi r^2$. The radius of a circle is just a difference between two points. The error on A, σ_A , is the

partial derivative:

$$\sigma_A = \frac{\partial A}{\partial r} \cdot \sigma_r = 2\pi r \cdot \sigma_r \quad \text{Eq. 3}$$

and $\sigma_r = \sqrt{30^2 + 30^2}$ (m). Error estimates on patch based nearest neighbor distances (NN) are simply a difference between two points. $\sigma_{NN} = \sqrt{30^2 + 30^2}$ (m).

Landscape metric error estimates

I estimated errors for landscape metrics for all habitat fragments combined since most landscape scale metrics are based on mean values over all patches.

A-Number of fragments (NP):

Before analyzing each landscape hexagon (at any of the 3 landscape sizes), I eliminated all fragments smaller than 2.5 ha because most of these fragments contained no core habitat (core area = 0). Therefore, since the digital maps had a resolution of 30m, I assumed that the error estimate on the number of fragments in a landscape was effectively nil.

B-Total area (TA), total core area (TCA) and forest cover (FC):

I estimated the error on the total area of all fragments in a landscape as if they were 1 fragment. The error estimate on TA was calculated as for the patch based error estimate on area above. I did the same for the

error estimate on forest cover (FC) which is $\sigma_{FC} = \sqrt{\left(\frac{\sigma_{TA}}{TA}\right)^2 + \left(\frac{\sigma_{TLA}}{TLA}\right)^2}$ (total landscape area (m)).

C-Mean patch size (MPS):

$$\sigma_{MPS} = \frac{\sigma_{TA}}{NP} \quad \text{Eq. 4}$$

D-Total edge (TE):

For each fragment in the landscape, edge = circumference (C) of the fragment (circular patch assumption) = $2\pi r$. Since $\sigma_C = 2\pi\sigma_r$, where $\sigma_r = \sqrt{30^2 + 30^2}$ (in m), I can calculate the error estimate for the edge of a single fragment in the landscape. Total Edge (TE) is the sum of the edge contributions of each individual fragment in the landscape, but I approximate it here as the average edge of a fragment.

$$\sigma_{TE} = NP * \sigma_C \quad \text{Eq. 5}$$

E-Mean nearest neighbour (MNN):

As before, the error estimate on NN is the difference between two point error estimates

$\sigma_{NN} = \sqrt{30^2 + 30^2}$ (m). At the landscape scale, the equivalent NN measure is an average for all fragments; therefore, I estimate the error as:

$$\sigma_{MNN} = \frac{\sqrt{30^2 + 30^2}}{NP} \quad \text{Eq. 6}$$

F-Mean proximity Index (MPI):

The proximity value P_i is calculated for each patch (in this case forest fragments) by locating all other

patches (i) within a specified distance buffer (in m) (Gustafson and Parker 1994):

$$P_x = \sum_{i=1}^n \frac{A_i}{z_i} \quad \text{Eq. 7}$$

where A_i and z_i are the area and edge to edge nearest neighbor distance of each of the n forest fragments located within the buffer. At the landscape scale, the mean proximity index is the average P_x for all patches in the landscape. Details for the calculation and interpretation of this metric can be found in Gustafson and Parker (1994). For the purposes of this study, I used MPS and MNN to estimate the error on MPI:

$$\sigma_{MPI} = \frac{\sigma_{MPS}}{\sigma_{MNN}} = \sqrt{\left(\frac{\sigma_{MPS}}{MPS}\right)^2 + \left(\frac{\sigma_{MNN}}{MNN}\right)^2} \quad \text{Eq. 8}$$

G- Principal component analysis (PCA):

I used the first two principal components as ranking variables for the nestedness calculations to represent independent measures of forest composition and configuration. Given a symmetric association matrix A , the terms located above and below the diagonal indicate the degree of association of the objects (landscape variables) under study (Legendre and Legendre 1998). With PCA, a diagonal matrix Λ is computed from the input covariance matrix of the raw variables with the eigenvalues λ_n of n components representing the diagonal elements:

$$A = \begin{bmatrix} a_{11} & a_{12} & \dots & a_{1n} \\ a_{21} & a_{22} & \dots & a_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ a_{n1} & a_{n2} & \dots & a_{nn} \end{bmatrix} \quad \Lambda = \begin{bmatrix} \lambda_{11} & 0 & \dots & 0 \\ 0 & \lambda_{22} & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & \lambda_{nn} \end{bmatrix} = \begin{bmatrix} \lambda_1 & 0 & \dots & 0 \\ 0 & \lambda_2 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & \lambda_n \end{bmatrix} \quad \text{Eq. 9}$$

The eigenvalues λ_n and eigenvectors u_n of matrix A are found from $Au_n = \lambda_n u_n$. The eigenvectors of the new matrix have the property of having completely linearly independent associations. Six variables were included in the PCA of this study: NP, MPS, TCA, TE, MPI and MNN. The variance of each principal component is given by the corresponding eigenvalue λ_n . By definition, the error on each component is then $\sqrt{\lambda_n}$. I used this as my estimate of error for each principal component used as a ranking variable in the nested subset analysis. Since $\sqrt{\lambda_k}$ is an exact measure of error, it is probably the single best reference point for the error analysis in this study.

TABLES AND FIGURES

Table 1. Summary statistics for patch scale variables calculated for all 144 forest fragments and fragment zones. Values in each cell are minimum, maximum and mean values, respectively from top to bottom.

Zone	1	2	3	4	5	6	All
% Forest cover	60.7	36.3	43.5	16.1	14.6	29.4	-
Fragments	10	45	6	21	50	12	144
Species Richness (SR)	20.0	10.0	15.0	7.0	8.0	14.0	7.0
	42.0	39.0	28.0	28.0	28.0	23.0	42.0
	29.6	21.7	22.7	14.1	17.3	18.8	19.4
Area (ha) (A)	5.6	3.4	8.7	2.3	4.9	6.8	2.3
	211.4	5139.6	79.0	196.7	123.5	598.9	5139.6
	63.7	185.8	41.5	23.9	22.1	75.6	81.2
Core Area (ha) (CA)	0.0	0.0	0.7	0.0	0.0	0.0	0.0
	110.8	2852.4	30.0	76.0	43.4	316.8	2852.4
	24.6	98.3	13.1	5.4	5.0	33.5	38.1
Nearest Neighbor distance (m) (NN)	43.3	42.4	74.9	41.1	130.5	79.3	41.1
	2355.2	5777.7	694.2	2785.5	4524.9	1661.3	5777.7
	1012.6	2863.7	235.7	1144.6	2246.7	726.4	1984.4

Table 3. Summary results for first 2 components from principal component analysis (PCA) for 500, 1000 and 5000 ha landscapes with results from linear regression between individual components and landscape forest cover.

	Landscape size (ha) / Principal component					
	500		1000		5000	
	1	2	1	2	1	2
Landscape Metrics						
No. Fragments (NF)	-0.17	-0.87	-0.21	-0.97	-0.23	-0.93
Mean fragment size (MPS)	0.92	0.33	0.89	0.34	0.92	0.31
Total Edge (TE)	0.59	-0.59	0.75	-0.52	0.93	-0.27
Mean Proximity Index (MPI)	0.95	0.14	0.91	0.19	0.92	0.08
Total Core Area (TCA)	0.98	0.05	0.95	0.12	0.95	0.12
Mean Nearest Neighbor (MNN)	-0.39	0.72	-0.64	0.62	-0.71	0.62
Eigenvalue	3.25	1.78	3.52	1.64	4.02	1.44
% Variance explained	54.1	29.6	58.7	27.3	67.0	24.0
Linear regression with forest cover	0.87, p<0.001	0.03, p=0.32	0.93, p<0.001	0.07, p=0.121	0.97, p<0.001	0.01, p=0.99
(R ² , p value ($\alpha=0.05$))						

Table 4. Bird species occurrences in forest fragments and landscapes. X's indicate that the species was not included in the analysis because it occurred in less than 5 or more than 95 % of fragments or landscapes. ^aDesignated forest bird species as determined by Villard et al. (1999) are ranked first followed by the other bird species considered in the study, ordered alphabetically by species code. 71 total species were included in analyses.

Species Code	Common name	Scientific name	Fragment or landscape occurrence				Forest Species
			fragments (n=144)	500 (n=40)	1000 (n=35)	5000 (n=20)	
BLCP	Brown Creeper	<i>Certhia americana</i>	0.15	0.30	0.37	0.55	*
BLGW	Black-throated Green Warbler	<i>Dendroica virens</i>	X	X	0.14	0.10	*
BLWS	Blues-and-white Warbler	<i>Mniotilta varia</i>	0.48	0.75	0.69	0.75	*
BLWS	Chestnut-sided Warbler	<i>Dendroica pensylvanica</i>	0.26	0.50	0.63	0.70	*
BLWS	Downy Woodpecker	<i>Picoides pubescens</i>	0.60	0.90	X	0.85	*
BLWS	Hairy Woodpecker	<i>Picoides villosus</i>	0.34	0.60	0.69	0.78	*
LEFL	Least Flycatcher	<i>Empidonax minimus</i>	0.26	0.48	0.57	0.55	*
OVEN	Ovenbird	<i>Seiurus aurocapillus</i>	0.66	0.78	0.83	0.85	*
PIWO	Pileated Woodpecker	<i>Dryocopus pileatus</i>	0.17	0.30	0.34	0.45	*
SOJA	Scarlet Tanager	<i>Paranga olivacea</i>	0.50	0.68	0.74	0.85	*
CTTU	Tanager	<i>Catharus fuscescens</i>	0.62	0.80	0.80	0.90	*
WICM	White-throated Nuthatch	<i>Sitta carolinensis</i>	0.72	0.95	0.89	0.90	*
WICM	Wood Thrush	<i>Herpocchia mustelina</i>	0.61	0.78	0.80	X	*
WICM	White-throated Sparrow	<i>Zonotrichia albicollis</i>	0.27	0.45	0.43	0.70	*
YDSU	Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	0.19	0.33	0.43	0.50	*
MEFL	Alder Flycatcher	<i>Empidonax alnorum</i>	X	0.15	X	0.30	
AMCB	American Crow	<i>Corvus brachyrhynchos</i>	0.35	0.63	0.63	0.85	
AMGF	American Goldfinch	<i>Carduelis tristis</i>	0.33	0.48	0.49	0.65	
AMRE	American Redstart	<i>Setophaga ruticilla</i>	0.15	0.30	0.34	0.50	
AMRB	American Robin	<i>Turdus migratorius</i>	0.94	X	X	X	
AMW	American Woodcock	<i>Scopus minor</i>	X	X	0.17	0.25	
BLCH	Black-chinned Cuckoo	<i>Coccyzus erythrophthalmus</i>	X	X	0.11	0.25	
BLWA	Blackburnian Warbler	<i>Dendroica fusca</i>	X	X	0.20	0.25	
BLCH	Black-capped Chickadee	<i>Parus atricapillus</i>	0.87	X	X	X	
BHCO	Brown-headed Cowbird	<i>Molothrus ater</i>	0.67	0.83	0.89	0.75	
BLJA	Blue Jay	<i>Cyanocitta cristata</i>	0.81	0.93	0.11	X	
BLCH	Belted Kingfisher	<i>Dolichonyx oryzivorus</i>	X	X	0.17	0.20	
BLTH	Brown Thrasher	<i>Toxostoma rufum</i>	0.19	0.38	0.49	0.70	
CAWA	Canada Warbler	<i>Wilsonia canadensis</i>	X	0.13	0.17	0.30	
CEWA	Cedar Waxwing	<i>Bombusilla cedrorum</i>	0.39	0.73	0.90	X	
CHSP	Chipping Sparrow	<i>Spizella passerina</i>	0.22	0.33	0.37	0.55	
COGR	Common Grackle	<i>Quiscalus quiscula</i>	0.40	0.63	0.71	0.85	
COYE	Common Yellowthroat	<i>Geothlypis trichas</i>	0.38	0.63	0.71	0.85	
ESKI	Eastern Kingbird	<i>Tyrannus tyrannus</i>	0.10	0.20	0.23	0.45	
ESPH	Eastern Phoebe	<i>Sayornis phoebe</i>	0.10	0.23	0.29	0.35	
ESWP	Eastern Wood-Pewee	<i>Contopus virens</i>	X	0.90	0.94	0.80	
ESST	European Starling	<i>Sturnus vulgaris</i>	0.19	0.43	0.49	0.45	
FSF	Field Sparrow	<i>Spizella pusilla</i>	X	X	X	0.10	
GCFL	Great Crested Flycatcher	<i>Myiarchus cinerascens</i>	0.92	X	X	X	
GCKI	Golden-crowned Kinglet	<i>Regulus satrapa</i>	X	X	0.14	0.15	
GRCA	Gray Catbird	<i>Dumetella carolinensis</i>	0.17	0.38	0.34	0.60	

Table 4 continued...

Species Code	Common name	Scientific name	Fragment or landscape occurrence				Forest Species*
			fragments (n=144)	500 (n=40)	1000 (n=35)	5000 (n=20)	
HETH	Hermit Thrush	<i>Catharus guttatus</i>	X	X	0.11	0.25	
HOSP	House Sparrow	<i>Passer domesticus</i>	X	X	X	0.10	
HOWR	House Wren	<i>Troglodytes aedon</i>	X	X	0.17	0.25	
INBU	Indigo Bunting	<i>Passerina cyanea</i>	0.20	0.35	0.43	0.60	
MAWA	Magnolia Warbler	<i>Dendroica magnolia</i>	X	0.15	0.23	0.25	
MOBO	Mourning Dove	<i>Zenaidura macroura</i>	X	0.18	0.23	0.40	
MOWA	Mourning Warbler	<i>Oporornis philadelphia</i>	0.21	0.53	0.51	0.70	
NAWA	Nashville Warbler	<i>Vermivora ruficapilla</i>	0.11	0.18	0.31	0.30	
NOCA	Northern Cardinal	<i>Cardinalis cardinalis</i>	X	X	0.17	0.20	
NOOB	Northern Oriole	<i>Icterus galbula</i>	0.67	0.88	0.94	0.85	
NOFA	Northern Parula	<i>Parula americana</i>	X	X	X	0.10	
NOWA	Northern Waterthrush	<i>Seiurus noveboracensis</i>	0.13	0.30	0.34	0.50	
OSFI	Olive-sided Flycatcher	<i>Contopus borealis</i>	X	X	X	0.10	
PEWA	Pine Warbler	<i>Dendroica pinus</i>	X	X	0.17	0.30	
PLFI	Purple Finch	<i>Carpodacus purpureus</i>	0.11	0.18	0.26	0.35	
REBF	Red-breasted Grosbeak	<i>Phaethon ludovicianus</i>	0.85	X	0.89	X	
REBN	Red-breasted Nuthatch		0.15	0.28	0.31	0.45	
REVI	Red-eyed Vireo	<i>Vireo olivaceus</i>	0.94	X	X	X	
RSLO	Rufous-sided Towhee	<i>Pipilo erythrophthalmus</i>	X	X	0.11	0.10	
RTHC	Ruby-throated Hummingbird	<i>Archilochus colubris</i>	X	X	0.11	0.20	
RWBH	Red-winged Blackbird	<i>Agelaius phoeniceus</i>	0.36	0.65	0.57	0.70	
SONI	Song Sparrow	<i>Melospiza melodia</i>	0.73	0.95	0.83	X	
STAB	Starling	<i>Sturnus vulgaris</i>	X	X	X	0.10	
SWSE	Swamp Sparrow	<i>Melospiza georgiana</i>	X	X	0.11	0.25	
SWTH	Swainson's Thrush	<i>Catharus ustulatus</i>	X	X	0.11	0.20	
WAVI	Warbling Vireo	<i>Vireo gilvus</i>	0.26	0.45	0.40	0.60	
WWEF	Winter Wren	<i>Troglodytes troglodytes</i>	0.10	0.15	0.29	0.40	
YBWA	Yellow-rumped Warbler	<i>Dendroica coronata</i>	X	0.10	0.14	0.30	
YNEI	Northern Flicker	<i>Colaptes auratus</i>	0.51	0.80	0.77	0.85	
YWWE	Yellow Warbler	<i>Dendroica petechia</i>	X	0.23	0.17	0.35

Figure 1. Study region near Ottawa, Ontario. Dataset includes 144 forest fragments surveyed for birds and which can be grouped into 6 forest fragment zones representing a gradient of decreasing forest cover and increasing fragmentation.

Figure 2. Relationship between NS_a and PN_0 standardized nestedness metrics and % forest cover for all species ranked by species richness for the six forest fragment zones. Both indices control for differences in the number of sites while NS_a also accounts for differential incidences between species.

Figure 3. Frequency distribution of total species richness for the 144 forest fragments in the dataset.

Figure 4. Distribution of the proportion of forest cover in A-500, B-1000 and C-5000 ha landscapes containing at least 2 surveyed forest fragments. 500 ha landscapes are nested within 1000 ha landscapes and 1000 ha landscapes are nested within 5000 ha landscapes.

Figure 5. Linear regression of log (area) and log (species richness) for 144 forest fragments in the dataset (R^2 : 0.36, s.e.: 0.270, $p < 0.001$, $\alpha = 0.05$).

Figure 6. Relationship between total or mean species richness in a forest fragment zone and A-forest cover (within a 10 km radius circle centered on each fragment cluster (zone)), B-number of surveyed forest fragments in a zone and C-standardized nestedness for each zone (PN₀).

Figure 7. Standardized nestedness (PN_0) with forest fragments ranked by a-species richness, b-area, c-core area and d-nearest neighbor distance of forest fragment larger than 30 ha, for A-all bird species (n=46) and B-forest bird species only (n=14).

Figure 8. Standardized nestedness (PN_0) for landscapes ranked by several landscape scale variables (see table 3 for variable description) and independent measures of forest composition (cover) and configuration (fragmentation) [PCA1 and PCA2, respectively] for 500 (A,D), 1000 (B,E) and 5000 (C,F) ha landscapes including all bird species (A,B,C) and forest bird species only (D,E,F).

Figure 9. Standardized partial nestedness scores of 14 forest bird species for forest fragments ranked by species richness (SR), area (A), core area (CA) and nearest neighbor distance of a forest fragment larger than 30 ha (NN) for A-all forest fragments. B-zone 2 (forest cover: 36.3%) and C-zone 5 (forest cover: 14.6 %). To facilitate interpretation, bars show $(1 - [N_0 / \# \text{ absences}])$. Details on the interpretation of scores and no data values in text.

Figure 10. Standardized partial nestedness scores of 13 forest bird species for landscapes ranked by species richness (SR) and independent measures of forest composition (cover) and configuration (fragmentation) [PCA1 and PCA2, respectively] for 500 (A), 1000 (B) and 5000 (C) ha landscapes. To facilitate interpretation, bars show $(1 - [N_i / \# \text{absences}])$. Details on the interpretation of scores and no data values in text.

Figure 11. Mean standardized partial nestedness scores ranked by species richness (SR) of forest bird species grouped by migratory strategy (LD-long distance migrant, SD-short distance migrant, and R-Resident). A- patch based design: all forest fragments, zone 2 (forest cover: 36.3%) and zone 5 (forest cover: 14.6 %), and B-Landscape scale design: 500, 1000 and 5000 ha landscapes. To facilitate interpretation, bars show $(1-[N_0/\#absences])$. Details on the interpretation of scores and no data values in text.

Figure 12. Effect of measurement error as the absolute value of Z (solid line) between observed and expected standardized nestedness scores, on forest fragment sites ranked by species richness (SR), area (A) and nearest neighbor distance of a forest fragment larger than 30 ha (NN). Left column plots are for zone 3 (6 fragments) and zone 5 for the right column (50 fragments). Plotted error values for all ranking variables range between 0 to 2.5 standard deviations. Error on species richness is based on a simple equiprobable estimate of undetected species for the entire regional species pool ranging between 0 and 20%. Relative nestedness scores (PN_0) across the error range (line with filled circles) are also shown.

Figure 13. Effect of measurement error on the absolute value of Z (solid line) between observed and expected standardized nestedness scores, on 5000 ha landscapes (forest bird species only) for landscapes ranked by species richness (SR), mean forest fragment size (MPS), total area (TCA), total edge (TE), nearest neighbor distance of a forest fragment larger than 30 ha (MNN), mean proximity index (MPI), total core area (TCA) and independent measures of forest composition (cover) and configuration (fragmentation) [PCA1 and PCA2, respectively]. Plotted error values for all ranking variables range between 0 and 2.5 standard deviations. Error on species richness is based on a simple equiprobable estimate of undetected species for the species pool ranging between 0 and 20%. Relative nestedness scores (PN₀) across the error range (line with filled circles) are also shown.

Figure 14. Difference in standardized partial nestedness between all fragments and a forest fragment zone ($PN_{0(T)} - PN_{0(Z)}$) for 14 forest birds. Zone 2 ($n=45$) and Zone 5 ($n=50$) are shown.