INDEPENDENT EFFECTS OF HABITAT AMOUNT AND FRAGMENTATION ON SONGBIRDS IN A FOREST MOSAIC: AN ORGANISM-BASED APPROACH

Matthew G. Betts[†] (corresponding author)

Faculty of Forestry and Environmental Management

University of New Brunswick

G.J. Forbes

Faculty of Forestry and Environmental Management

University of New Brunswick

A.W. Diamond,

Atlantic Cooperative Wildlife Ecology Research Network

University of New Brunswick

Phillip D. Taylor

Atlantic Cooperative Wildlife Ecology Research Network

Acadia University

[†] Address for correspondence: 1350 Regent St., Fredericton, New Brunswick, Canada, E3C 2G6, m.betts@unb.ca

Abstract. The degree to which spatial patterns influence the dynamics and distribution of populations is a central question in ecology. This question is even more pressing in the context of rapid habitat loss and fragmentation which threaten global biodiversity. However, the relative influence of habitat loss and landscape fragmentation – the spatial patterning of remaining habitat – remains unclear. If landscape pattern affects population size, managers may be able to design landscapes that mitigate habitat loss. We present the results of a mensurative experiment designed to test four habitat loss versus fragmentation hypotheses. Unlike previous studies, we measured landscape structure using quantitative, spatially explicit habitat distribution models previously developed for two species: blackburnian warbler (*Dendroica fusca*) and ovenbird (*Seiurus aurocapillus*). We used a stratified sampling design that reduced the confounding of habitat amount and fragmentation variables. Occurrence and reoccurrence of both species were strongly influenced by characteristics at scales greater than the individual territory, indicating little support for the random sample hypothesis. However, the type and spatial extent of landscape influence differed. Both occurrence and reoccurrence of blackburnian warblers were influenced by the amount of poor-quality matrix at 300 and 2000 m spatial extents. The occurrence and reoccurrence of ovenbirds depended on a landscape pattern variable – patch size – but only in cases when patches were isolated. These results support the hypothesis that landscape pattern is important for some species only when the amount of suitable habitat is low. Though theoretical models have predicted such an interaction between landcape fragmentation and composition, to our knowledge this is the first study to report empirical evidence of such non-linear fragmentation effects. Defining landscapes quantitatively from an organism-based perspective may increase power to detect fragmentation effects, particularly in forest mosaics where boundaries between patches and matrix are ambiguous. Our results indicate that manipulating landscape pattern may reduce negative impacts of habitat loss for ovenbird, but not blackburnian warbler. We emphasize that most variance in the occurrence of both species was explained by local scale or landscape composition variables rather than variables reflecting landscape pattern.

Key words: Fragmentation, habitat loss, landscape composition, organism-based, patch size, edge effect, matrix, blackburnian warbler, ovenbird.

INTRODUCTION

The degree to which spatial patterns influence the dynamics and distribution of populations is a central question in ecology (Turner 1989, Levin 1992). This question is even more pressing in the context of rapid habitat loss and fragmentation (FAO 2001, Matthews et al. 2001) which are considered principle threats to biodiversity globally (Pimm 1995). It is not surprising that habitat loss has been found to result in population declines (Balmford et al. 2003); behavior (Pulliam and Danielson 1991) and resource availability limit the degree to which increases in population density compensate for reduced habitat area. However, fragmentation, the process of subdividing contiguous habitat into smaller, isolated patches (*sensu* Fahrig 1998), may result in decreased patch colonization and increased rates of local extinction, both of which can result in population declines greater than expected from habitat loss alone (Hanski and Ovaskainen 2000).

Determining the relative importance of habitat loss versus fragmentation has been problematic. Because fragmentation occurs through a process of habitat loss in most circumstances, the effects of habitat amount (landscape composition) and fragmentation (landscape configuration) are usually confounded. Simulation modelling studies have addressed this problem by designing artificial landscapes that separate these variables (Fahrig 1998, Hill and Caswell 1999, With and King 1999, Flather and Bevers 2002, Wiegand et al. 2005). In these studies the relative importance of fragmentation appears to depend on the life histories of hypothetical species (Fahrig 1998, With and King 1999). Thresholds have been demonstrated to occur where the influence of fragmentation increases as the amount of suitable habitat decreases in the landscape (Hill and Caswell 1999, Flather and Bevers 2002). However, few empirical studies have been designed to test for the independent effects of landscape composition and configuration (Fahrig 2003). Several of these indicate that habitat amount is the dominating influence on population persistence (McGarigal and McComb 1995, Trzcinski et al. 1999, Heikkinen et al. 2004), but evidence is not unanimous (Villard et al. 1999, Krawchuk and Taylor 2003). As in simulation studies, the inconsistency in reported fragmentation effects has been attributed to variability in species' adaptations (e.g., movement ability, home range size, sensitivity to edge; Trzcinski et al. 1999).

Variable influences of landscape composition and configuration may also be due to the way in which landscapes have been measured and defined. The theory of island biogeography (MacArthur and Wilson 1967) and metapopulation theory (Levins 1969) form the conceptual underpinnings of landscape ecology, but both are based on simple binary landscapes made up of islands/patches (habitat) and ocean/matrix (non-habitat). While these are easily defined in island archipelagos or simulation models, identifying patches and matrix in real landscapes is often subjective (e.g., Homan et al. 2004, Suorsa et al. 2005) and may not be based in accurate estimates of what a species considers to be habitat (Addicott et al. 1987, Wiens et al. 1993, Wiens 1994). This problem is magnified in forest mosaics where habitat fragments are rarely surrounded by an ecologically neutral or inhospitable environment, and sharpness of edges varies with forest regeneration and succession (Bunnell 1999, Schmiegelow and Mönkönen 2002). The weakness of the patch-oriented approach is that it has failed to capture how individual species perceive and use heterogeneous landscapes (Wiens et al.1993, Ricketts 2001). Quantitative definitions of suitable habitat at the landscape scale (Boyce and McDonald 1999) offer potential to overcome this weakness. Such spatially explicit habitat models allow more accurate definitions of landscape structure (e.g., patch, matrix, edge) from the perspective of individual organisms (Moilanen and Hanski 1998).

The potential influences of landscape composition and configuration on populations can be expressed as four competing hypotheses, each with different implications for how habitat loss and fragmentation affect populations.

The *random sample hypothesis* states that small patches are simply random samples of larger patches (Haila 1983). Only factors at the local scale (the spatial extent of individual territories) are important in determining habitat quality. Thus, habitat loss produces a proportional decline in the number of animals living in a particular landscape.

In the *landscape composition hypothesis*, the amount of habitat is important, but at larger spatial scales than the individual territory (Fahrig 2003). This distribution pattern could result from preferences of dispersing individuals for breeding sites that are in proximity to conspecifics or heterospecifics (Mönkkönen et al. 1999, Danchin et al. 2004). Large year-to-year environmental variation and short breeding season presumably render such habitat-selection behavior beneficial. Alternatively, movement of organisms could be restricted if there is a large amount of impervious matrix (non-habitat) (Jonsen and Taylor 2000, Goodwin and Fahrig 2002). In a special case of landscape composition hypothesis, abundance of higher quality matrix could decrease the need for habitat at the territory scale. Animals may supplement resources by using the surrounding matrix (Andrén et al 1997, Tubelis et al. 2004).

The *landscape fragmentation hypothesis* expects populations to decline linearly with fragmentation, independent of the effects of habitat loss (Villard et al. 1999). Fragmentation effects could result from increased amount of edge, which in some contexts has been found to increase predation (Bátary and Báldi 2004, Marzluff et al. 2004) and reduce food availability (Burke and Nol 1998). Alternatively, fragmentation effects could result from decreases in patch size. Bender et al. (1998) argued that many reported patch size effects could be due simply to increased edge effects in small patches (the geometric effect). Nevertheless, patch size effects could occur independently of edge effect. For species that are reluctant to cross gaps (Desrochers and Hannon 1997), conspecific and heterospecific attraction could result in the selection of larger patches (Connor et al. 2000). Root (1973) argued that densities of organisms might be higher in large patches as a result of increased attraction of moving individuals. Others have predicted that smaller patches should exhibit higher densities due to higher chances of intercepting ground-level dispersers (Bowman et al. 2002), or reduced interspecific competition (MacArthur et al. 1972). Non-threshold landscape configuration effects will result in additive population declines above those that occur as a result of habitat loss.

The *non-linear fragmentation hypothesis* states that landscape configuration is important only below some critical amount of suitable habitat (Andrén 1994, Fahrig 1998, Flather and Bevers 2002). Only at low levels of habitat are patches small and isolated enough to result in patch size effects or restrictions in movement (Gardner et al. 1991). This will result in multiplicative (non-linear) effects of fragmentation on habitat loss (i.e., a statistical interaction between landscape configuration and composition).

Here, we present the results of a mensurative experiment designed to test these four habitat loss versus fragmentation hypotheses. To do this, we investigated the independent effects of commonly reported composition (amount of suitable habitat, poor-quality matrix) and configuration variables (patch size, edge effect) on the distribution of two species of forest songbirds: blackburnian warbler (*Dendrioca fusca*) and ovenbird (*Seiurus aurocapilla*). Both species are associated with mature forest (Betts et al. *In Press*), are deemed to be area sensitive (Freemark and Collins 1992), and have been in decline in New Brunswick, Canada from 1983-2003 (Sauer et al. 2004) possibly as a result of habitat decline on the breeding grounds (Betts et al. 2003). Unlike previous studies, we adopted a quantitative organism-based approach that relied on independently derived (Betts et al. *In Press*), spatially explicit habitat distribution models to test the effects of landscape composition and configuration.

METHODS

Study area

The study was conducted in the Greater Fundy Ecosystem, New Brunswick (NB), Canada (66.08^{o}– 64.96^{o}, 46.08^{o}– 45.47^{o}) (~4000 km^2). The Greater Fundy Ecosystem is characterized by 89% forest cover, a maritime climate, and rolling topography (elevation 70 – 398m). Forest cover is primarily sugar maple (*Acer saccharum* Marsh.), beech (*Fagus grandifolia* L.), yellow birch (*Betula alleghaniensis* Britt.), red spruce (*Picea rubens* Sarg.), and balsam fir (*Abies balsamea* (L.) Mill.). However, black spruce (*P. mariana* Mill.) exists in low-lying areas. Intensive forestry activities (i.e., clearcutting, spruce and pine planting, thinning) have occurred since the early 1970s, resulting in a heterogeneous landscape mosaic where approximately 40% of the study area is mature (>70 years), unmanaged forest (NBDNR 1993).

Spatially explicit habitat models

In a separate study, we developed spatially explicit habitat models for the occurrence of both bird species using local-scale variables derived from GIS as predictor variables (Betts et al. *In Press*) (equations 1 and 2).

$$\hat{p} \text{ (blackburnian warbler occurrence)} = 1/ (\exp (3.58 +15.63(R) +1.63(S) +0.82(Y) -0.62(M) -1.42(O) -0.61(CC) -0.17(Slope)) + 1) \quad (1)$$

$$\hat{p}\text{ (ovenbird occurrence)} = 1/ (\exp (1.50 +1.79(R) +1.52(S) +0.29(Y) -0.66(M) -1.29(O) +0.06(IMW) +2.86(PINE) +2.95(SW) + 0.92(TMW) -0.82(CC)) + 1) \quad (2)$$

Where R, S, Y, M, and O are age class variables representing regenerating, sapling, young, mature, and overmature respectively; CC = crown closure; Slope = slope in degrees; IMW, PINE, SW, and TMW are cover type variables representing shade-intolerant mixedwood, pine, softwood, and shade-tolerant mixedwood, respectively (see Betts et al. *In Press* for age class and cover type details).

GIS land cover data originated from the New Brunswick Forest Inventory (NBDNR 1993), which is based on interpreted and digitized aerial photographs taken in 1993 (1:12,500 scale, colour) and updated to 2000 with satellite imagery (30 m^2 resolution; Betts et al. 2003). We used Receiver Operating Characteristic curves as a measure of habitat model accuracy. The Area Under the Receiver Operating Characteristic Curve (AUC) describes the relationship between the sensitivity (number of positive observations correctly predicted as positive) and specificity (number of false positive predictions; Hanley and McNeil 1982). The AUC is a single index of classification accuracy that ranges from 0 – 1, and is independent of species prevalence and arbitrary threshold effects (Manel et al. 2001). Models exhibited adequate prediction success (Hosmer and Lemeshow 2000) when tested on independent data from within the Greater Fundy Ecosystem study area (blackburnian warbler AUC = 0.786±0.03 SE, ovenbird AUC = 0.831±0.026 SE) and on independent data from a geographically distinct study area (blackburnian warber AUC = 0.670±0.05 SE, ovenbird AUC = 0.819±0.035 SE; Betts et al. *In Press*).

Landscape variables and study design

Using spatially explicit habitat models, we then developed habitat suitability maps (30 m^2 resolution) from local-scale GIS models for both blackburnian warbler and ovenbird. These maps were used to identify two landscape configuration variables (patch size, distance from edge) and two landscape composition variables (habitat amount, poor-quality matrix) that are the most likely to influence distribution of forest songbirds (Appendix A; Lichstein et al. 2002a).

To identify habitat patches in the forest mosaic we determined cut points in estimated habitat suitability ($\hat{p}$) using Receiver Operating Characteristic curves; cut points were identified where the sum of model sensitivity and specificity was maximized (Guénette and Villard 2005). This approach may overestimate habitat for rarer species, but results in higher prediction success than the use of arbitrary cut points (e.g., $\hat{p}$ =0.5; Manel et al. 2001). Cut point values were $\hat{p}$ =0.41 and $\hat{p}$ =0.47 for blackburnian warbler and ovenbird respectively. As predictive ability of both models was adequate, according to estimates of AUC (see *Spatially explicit habitat models*), we consider these cut points to be reliable. Patch size was measured as the total area of suitable habitat that is separated from other patches by >30 m. Territories of our focal species are unlikely to span gaps of these size (after Villard et al. 1995).

We summed the amount of habitat, weighted by $\hat{p}$, at two spatial extents for all locations within our study area (300 m, 2000 m radii). These extents reflect those previously found to influence forest passerine habitat use (Drapeau et al. 2000, Mitchell et al. 2001), and likely include the spatial extents relevant to migrant warblers in natal dispersal (Bowman 2003), and extra-territorial movements (Norris and Stutchbury 2001).

We used a randomized stratified sampling design so that samples represented the range of variation in patch size and habitat amount at landscape extents (hereafter “habitat amount”). To serve as a basis for sampling, we defined five patch size categories: 1–20 ha, 21–50 ha, 51–100 ha, 101–500 ha, <500 ha, and three habitat amount categories: 0–30%, 31–70%, 71–100%. For the purposes of study design we used the greatest spatial extent (2000 m) to measure habitat amount. We selected sample patches that ensured that all possible combinations of patch size and habitat amount were represented. This involved searching for locations with poorly represented combinations of habitat amount and patch size so that the expected positive correlation between habitat loss and fragmentation was reduced (after Trzcinski et al. 1999). We also selected patches that had the least ambiguous boundaries (i.e., where differences in $\hat{p}$ between within patch habitat, and adjacent non-habitat were greatest). In total, 187 blackburnian warbler and 214 ovenbird patch/landscape combinations were sampled in 2002. Timber harvesting reduced the number of patches to 179 and 203 for blackburnian warbler and ovenbird respectively.

In each patch, we established 1–4 sample points beginning 75 m from clearly identifiable forest edges (i.e., roads, recent clearcuts [<10 years]) and proceeding at 250 m intervals toward the patch center. In forest mosaics, such "hard" edges are the most likely to result in decreased habitat quality (Harris and Reed 2002, Manolis et al. 2002). If patches were surrounded by multiple hard edges, as was often the case, location of transect entry point was determined randomly. In 2002, we established 363 individual sample points in blackburnian warbler or ovenbird patches. In 2003, harvesting reduced these to 341.

To reflect matrix heterogeneity, we summed the amount of poor-quality matrix at all three spatial extents. We defined poor-quality matrix as areas with very low values of $\hat{p}$ (<95th percentile, $\hat{p}$ =0.05). Such poor quality matrix is most likely to be inhospitable for movement (Vega et al. 1998, Haddad and Baum 1999, Belisle and Desrochers 2002). The cut point for poor quality matrix had to be defined arbitrarily since, to our knowledge, no detailed analysis of movement cutpoints in relation to habitat suitability was available in the literature. However, the amount of poor-quality matrix was not highly sensitive to changes in cut point for blackburnian warbler (area $\hat{p}_{0.05} / \hat{p}_{0.1} = 0.793$) or ovenbird (area $\hat{p}_{0.05} / \hat{p}_{0.1} = 0.843$).

One drawback to a patch-based research design can be that landscape scale sample size is very low (because multiple patches exist within a single landscape), limiting the ability to make landscape-scale inferences (Fahrig 2003). We avoided this problem by characterizing the landscape surrounding each individual sample point and then accounting for lack of independence of points within a patch by using mixed models. The independence of the resulting landscapes were also tested using spatial autocorrelation (see *Statistical analysis*). A key advantage of this patch-based design was that it allowed us to precisely characterize, separate, and test the independent effects of fragmentation and habitat amount. Once patches are identified, patch size is an unambiguous and easily measured variable whereas landscape-scale patch metrics (e.g., mean patch size, patch size coefficient of variation) are both difficult to interpret (Gustafson 1998) and control for in study designs.

Bird sampling

We conducted fixed-radius point counts of forest passerines (Ralph et al. 1995) at each sample point within the period 03 June–11 July in both 2002 and 2003. Three counts of 5-minute duration were conducted on separate occasions between 05:30–11:00 AST. All male birds seen or heard during this time period within a 50 m radius were recorded as ‘present’. Birds flying overhead were not used in data analysis. Because mean bird counts per station tended to be low (<2) for both species, and because we were interested in estimating probability of occurrence, we reduced relative abundance data to presence/absence for use in binomial models. Because the number of times a bird is observed at a location in successive years may be an indicator of habitat quality (Hames et al. 2001, Rodenhouse et al. 2003), we also identified sites that were occupied by each species in both 2002 and 2003 (hereafter "reoccurrence").

Vegetation sampling

Evaluating the hypothesis that vegetation at the local scale alone can explain variation in forest bird occurrence (random sample hypothesis) required detailed information about vegetation composition and structure at local scales. At each point count location we counted and identified to species all woody stems >2cm diameter at breast height (dbh) within a 20 x 10 m plot (0.02 ha, 2.5% of 50 m point count circle; Bowman et al. 2001). To reduce variables used in analysis, we collapsed tree data into dbh categories: 10–30 cm dbh and >30cm dbh, and two species groups (coniferous, deciduous; Appendix A). We calculated basal area using all trees >2 cm dbh. Shrubs (woody stems < 2 cm diameter and > 0.5 m tall) were tallied in a 20 x 2 m plot nested within the larger plot. Canopy cover was estimated with a vertical viewing tube 10 cm long and 3 cm inside diameter and fitted with crosshairs. Readings were taken by counting the number of times crosshairs intersected with canopy foliage at 2 m intervals around the perimeter of the 20 x 10 m plot (Emlen 1967). We estimated the number of mature spruce (>20 cm dbh; a known requirement for blackburnian warbler nesting; Morse 1994, Young et al. 2005) within 50 m of each sample point. The number of spruce was recorded as one of the following density classes: 0, 1–5, 6–10, 11–50, 51–75, 76–100, >100 stems/ 50m radius point count plot (after Young et al. 2005).

For analysis, we selected habitat variables based on local scale habitat relationships observed in the study region (Betts et al. *In Press*) and elsewhere (for reviews see Morse 1994, Van Horne and Donovan 1994; Appendix A).

Statistical Models

Our study design made it necessary to account for the potential lack of independence among multiple points nested within a single patch. We applied generalized linear mixed models (GLMMs) using Penalized Quasi-Likelihood to determine parameter estimates. These models penalize estimated standard errors for potential lack of independence due to grouping, and are thus appropriate for modeling the dependence among outcome variables inherent in clustered data (see Breslow and Clayton 1993 for details). Individual patches were treated as random effects and all other variables as fixed effects. All models were fit in R 2.0.1 (R Development Core Team 2004) statistical program using the GLMM routine with a binomial family (Bates and Sarkar 2005).

We used the information-theoretic approach as a model selection procedure (Burnham and Anderson 2002). The advantage of this approach is that it allows one to measure and reflect model selection uncertainty. Models with lower Akaike's Information Criterion (AIC) values are better fitting and more importantly, the relative likelihood of each model in relation to the best model can be determined using evidence ratios derived from AIC values. The evidence ratio can be interpreted as the number of times less likely model *i* is than the model with the lowest AIC. In cases where model selection uncertainty existed, we used AIC weights to determine the relative importance of models. Weights were summed over the subset of models that included variable x_1. AIC weights can be interpreted as the Bayesian posterior probabilities for the model set, describing their relative likelihoods of best fitting the data (Zabel et al. 2003).

To test for the independent effects of landscape composition and configuration on the occurrence of both forest bird species, we used a sequential model-building approach. First, we fit models for occurrence and reoccurrence, using only local habitat variables. If two or more predictor variables were highly correlated ($r > 0.7$), we included variables that fit the data better (from visual inspections of residual plots and explained deviance). Because little model selection uncertainty existed among local habitat models for either species, we considered the best models to be the ones with the smallest AIC values.

Once best local models had been determined, we used AIC to assess the weight of evidence for, or against, four habitat loss versus fragmentation hypotheses. We applied the following model building approach: (1) To control for local-scale variability, best local habitat variables were always retained (Lichstein et al 2002b). (2) To avoid multicollinearity, we did not include any landscape habitat and poor-quality matrix variables from the same spatial extent in the same models. (3) Even though we explicitly designed our sampling to separate the confounding of configuration and cover, some degree of correlation occurred among landscape variables (Table 1). To consider the effects of landscape configuration over and above the influence of habitat amount, we included at least one large-extent habitat amount variable (2000 m) in addition to any configuration terms (Fahrig 2003, Krawchuk and Taylor 2003). (4) We evaluated the non-linear fragmentation hypothesis by examining interactions between both configuration variables (patch size, edge) and composition variables (habitat, poor-quality matrix amounts at a 2000 m extent) (Appendix A). Support for such an interaction would indicate a non-linear relationship between landscape composition and configuration and support for the non-linear fragmentation hypothesis (Tzrcinski et al. 1999). (5) If models with one or two landscape variables ranked within 4 AIC units of the best model, these were combined to determine if model fit could be improved (Zabel et al. 2003). These model-building rules resulted in a candidate set of 21–22 models for each species in each year and for reoccurrence. We did not detect overdispersion in either local or landscape GLMM models ($\hat{c} < 1$).

Collinearity in explanatory variables often hampers the detection of the independent effects of environmental variables. We used a variance partitioning approach (Chevan and Sutherland 1991, Borcard et al. 1992, MacNally 2000) to determine the independent contributions of local habitat, landscape composition, and landscape configuration variables to explained variance. Partial explained deviance values for local, landscape composition, and landscape configuration variables were calculated as the increase in explained deviance in logistic regression models due to the inclusion of variables from each predictor set after controlling for variables from all other sets (Venables and Ripley 2001).

The presence of spatial autocorrelation is not simply a statistical problem to be avoided – it can provide important information about the ecology of species (Legendre 1993). We used correlograms of Moran's *I* (hereafter *I*) to test for autocorrelation in Pearson residuals of all regression model sets (Kaluzny et al. 1996; Klute et al. 2002). We standardized *I* by dividing by its maximum value (after Haining 1990; Lichstein et al. 2002b). Because the shortest distance between sample points in both study areas was ~250–350 m, our lag intervals were at 350 m up to a maximum distance of 7000 m. We used randomization tests (999 permutations) to determine the probability of observing a value of *I* as large as the observed value. For each correlogram, the significance of *I* for each lag distance was calculated using a Bonferroni correction for multiple tests (after Lichstein et al. 2002b). To test the hypothesis that landscape composition effects may be due to aggregation (Lichstein et al. 2002b), we tested for spatial autocorrelation in residuals of bird habitat models that included only local-scale vegetation. Because GLMMs effectively removed all spatial dependency of points in proximity within the same patch (see *Results*), we used fixed effects models (GLMs) in these tests for spatial autocorrelation. We predicted that local models should exhibit spatial autocorrelation, but that the inclusion of landscape terms should account for this aggregative effect.

RESULTS

Blackburnian warbler

Blackburnian warbler occurrence and reoccurrence at the local scale tended to be associated with large (>30 cm dbh) tree density, mixed coniferous-deciduous forest, and a high percentage of canopy cover (Table 2). However, we found little support for the random sample hypothesis; the model including only local variables tended to perform poorly and was 167.7 (ΔAIC 10.23), 11.9 (ΔAIC 4.95) and 40.0 (ΔAIC 7.37) times less likely to fit the data than the top-ranked model in 2002, 2003 and for reoccurrence respectively (Table 3). Evidence from AIC and variance partitioning supported the landscape composition hypothesis. Occurrence of blackburnian warbler in both years and reoccurrence was best predicted by models containing only landscape composition variables (2002: top 4 models $\sum w_i = 0.753$; 2003: top 3 models $\sum w_i = 0.692$; reoccurrence: top 5 models $\sum w_i = 0.745$; Appendices B-D). The contribution of landscape variables to independently explained variance in blackburnian warbler occurrence was 25% (2002), 22% (2003) and 29% (reoccurrence; Fig. 1A). Models containing fragmentation variables tended to have only weak support and explained little variance (Table 3, Fig. 1). Thus, in this species, there was little support for either the fragmentation or non-linear fragmentation hypothesis.

We found considerable uncertainty about the most important spatial extent for blackburnian warbler. Occurrence in 2002 and reoccurrence were best predicted by the amount of poor-quality matrix at both 300 m and 2000 m spatial extents (Table 2, Appendices B and D. Controlling for local-scale variation, the species was less likely to occur and reoccur in landscapes with large amounts of matrix at these extents. In 2003, the best model indicated that the occurrence of blackburnian warbler was most reliably predicted only by the amount of matrix within 300 m (Table 2, Appendix C).

Ovenbird

Ovenbird occurrence and reoccurrence at the local scale was positively correlated with canopy cover, basal area of deciduous trees and leaf litter (Table 4). However, as with blackburnian warbler, we found little support for the random sample hypothesis; the ovenbird model including only local variables was not supported in 2002 (evidence ratio [ER]: 28 991.3, ΔAIC 20.55), or for reoccurrence (ER: 30.7, ΔAIC 6.85; Table 5), but had weak support in 2003 (ER: 6.7, ΔAIC 3.79). The proportion of variance independently explained by landscape variables was 62%, 63% and 65% for 2002, 2003, and reoccurrence respectively (Fig. 1B).

We found considerable support for the non-linear fragmentation hypothesis for ovenbird. The occurrence of this species in 2002 and reoccurrence was best predicted by both composition and configuration variables (Table 5, Appendices E and G); AIC weights of models containing interactions between landscape configuration and composition constituted the best two models in 2002 ($\sum w_i = 0.973$) and the best three models for reoccurrence ($\sum w_i = 0.881$; Appendices E and G). However, in 2003, models supporting the landscape composition hypothesis were reasonable competitors with the composition-configuration interaction models (interaction models $\sum w_i = 0.414$, composition models $\sum w_i = 0.358$; Appendix F). We found very little support for the fragmentation hypothesis; models containing configuration variables in the absence of composition-configuration interaction terms were not supported (Table 5).

Patch size, rather than edge effect was the most important configuration variable in ovenbird models; edge effect appeared in none of the top models (ΔAIC<4) in 2002 or for reoccurrence and only one of the top models in 2003 (ΔAIC=3.7; Appendices E-G). Ovenbird was less likely to occur in small patches, but only when those patches were isolated (i.e., in landscapes containing relatively small amounts of habitat at the 2000 m spatial extent; Fig. 2). In 2002, ovenbird occurrence was positively correlated with the amount of habitat at both 300 m and 2000 m spatial extents (Table 4). However, there was variation in the relative importance of these extents between years and for reoccurrence (Table 4, Appendices E-G).

Spatial autocorrelation

We did not detect spatial autocorrelation in the residuals of either local or landscape GLMMs for blackburnian warbler or ovenbird. Nor did we detect spatial autocorrelation in ovenbird GLMs including landscape variables; residuals showed little spatial pattern, indicating that the assumption of independent errors was not violated (Lichstein et al. 2002b). However, residuals of local-scale fixed effects models (GLMs) were spatially autocorrelated for ovenbird in 2002 (350 m: I=0.16, P=0.01), 2003 (350 m: I=0.12, P=0.04; 700 m: I=0.18, P=0.003) and reoccurrence (700 m: I=0.13, P=0.02) and for blackburnian warbler in 2002 (700 m: I=0.17, P=0.001, 1400 m: I=0.19, P=0.002). Top-ranked fixed effects models that included landscape variables exhibited spatial autocorrelation in residuals only in 2002 for blackburnian. In this case, autocorrelation existed to a lesser degree than in the local-scale model and at only one distance (700 m: I=0.15, P=0.01).

DISCUSSION

Landscape effects and the random sample hypothesis

Our results provide little support for the random sample hypothesis. Occurrence and re-occurrence of both species depended on forest characteristics at spatial extents greater than the individual territory. This suggests that forest landscape data do not consistently match the random sample hypothesis (*contra* Mönkkönen and Reunanen 1999). More recent studies conducted in forest mosaics have found that variables at landscape extents are significant predictors of bird occurrence. However, the importance of landscape variables has tended to be substantially less than local variables (Norton et al. 2000, Hagan and Meehan 2002). For instance, Lichstein et al. (2002a), one of the few forest mosaic studies to use a variance partitioning approach, found that landscape variables accounted for 0-24% of independently explained variance. Our results for blackburnian warbler are similar; the amount of variance explained by landscape variables was low in comparison to local scale variables (22-29%). However, over 60% of the independently explained variance in ovenbird occurrence was due to landscape variables. Comparatively strong landscape effects in our study are likely due to three non-mutually exclusive factors.

First, our samples were located in a subset of the entire forest where previously derived local-scale statistical models predicted the occurrence of both species (Betts et al. *In Press*). Several previous studies have commonly sampled all broadly-defined cover types within a high contrast forest (e.g., Drapeau et al. 2000, Lichstein 2002a). Because nesting and foraging requirements of many bird species are relatively stereotyped (Holmes and Sherry 1986), it is not surprising that landscape variables have been found to be comparatively less important; if appropriate nesting and foraging substrate are not available, a species is unlikely to occur regardless of how much appropriate habitat there is at broader spatial extents. However, in the current study, we held local level variation constant through a combination of study design and statistical control, which provided more power to detect landscape effects.

Second, detection of only minor landscape effects may result from a relatively high proportion of suitable habitat in a study landscape (Tewksbury et al. 1998, Norton et al. 2000, Lichstein et al. 2002a). In a simulation study, Andrén (1996) found that power to reject the random sample hypothesis is lower in landscapes with high proportions of suitable habitat. In our study, the range in the proportion of suitable habitat at the largest spatial extent was broad for both species (blackburnian warbler $\bar{x}$=28.5±5.0%, range=9.2-57.1%; ovenbird $\bar{x}$=37.9±0.7%, range=11.6-74.7%; percentages were calculated using amount of highest quality habitat [$\hat{p}$ =1.0] within 2000 m as a denominator). These values encompass the range of values (Andrén 1996) that would allow detection of landscape effects for species that are either area sensitive or poor dispersers.

Third, quantitative, organism-based approaches to defining landscape characteristics are still rare (Reunanen et al. 2002). Such an approach is particularly important in a forest mosaic where distinctions between habitat and matrix are less discrete than in agricultural mosaics or island archipelagos (Mönkkönen and Reunanen 1999). Previous studies have relied on arbitrary, or at least general definitions of suitable habitat at landscape extents (Trzcinski et al. 1999, Fischer et al. 2004).

Landscape composition versus fragmentation hypotheses

Through a combination of study design and statistical methods, we separated the often-confounded effects of landscape configuration and composition. The two species we examined responded to landscape structure differently. After controlling for local habitat and landscape composition, blackburnian warbler models containing configuration variables had very little support; our results for this species support the landscape composition hypothesis. Hagan and Meehan (2002) and MacFaden and Capen (2002) found weak, but significant landscape composition effects on this species. The lack of configuration effects is consistent with most studies that have attempted to separate the effects of habitat loss from fragmentation *per se* (see Fahrig 2003 for review).

In contrast, ovenbird distribution in 2002 and reoccurrence were strongly influenced by landscape pattern. We found a positive influence of patch size on ovenbird occurrence, but only when the amount of suitable habitat in the landscape was low. This result supports, for the first time to our knowledge, the non-linear fragmentation hypothesis (Fahrig 2003). In forest-agricultural landscapes, Villard et al (1999) found this species to be positively correlated with the amount of forest cover at the 2.5 x 2.5 km extent, but not with fragment area or edge effect. Several studies have reported greater likelihood of ovenbird occurrence in contiguous forest than in small, isolated patches (Hannon and Schmiegelow 2002, Nol et al. 2005). Lee et al. (2002) found that forest cover explained the most variation in ovenbird abundance, but that ovenbird density was lower in large patches. Lee et al. (2002) speculated that this negative patch size effect was due to habitat supplementation from foraging outside of small patches. However, none of these studies tested for interactions between patch size and habitat amount (a non-linear effect).

Numerous theoretical studies have found non-linear responses by species to fragmentation (Fahrig 1998, With and King 1999, Flather and Bevers 2002, Wiegand et al. 2005). Thresholds have been predicted to occur for species with low vagility, non-ephemeral habitat, high site-fidelity, and high mortality in non-breeding habitat areas (Fahrig 1998). Given this narrow range of conditions, and the logistical difficulty of separating the confounding effects of landscape composition and configuration, it is perhaps not surprising that few empirical studies have reported evidence for non-linear fragmentation effects. Ovenbirds are site faithful (Van Horne and Donovan 1994) and establish territories in deciduous forest, a forest type that is relatively stable (Lorimer 1977). However, dispersal distances of juveniles, and mortality in the matrix are unknown (Villard et al. 1995). More information on these life history characteristics is required before the conditions of fragmentation sensitivity put forward by theoretical models can be validated.

We found almost no support for pure fragmentation effects, uninfluenced by the amount of suitable habitat, for either species. This is consistent with numerous studies (Sallabanks et al. 2000, Drapeau et al. 2000, MacFaden and Capen 2002, but see Villard et al. 1999). The lack of support for the fragmentation hypothesis has been anticipated by a number of researchers since the initial stages of habitat loss, patches remain relatively well connected (Turner et al. 1989, Gardner et al. 1991). Thus, if the amount of suitable habitat in landscape is high, species are unlikely to respond to, or even perceive, gaps between patches.

Inferring process from pattern

In simulation studies, metrics summarizing habitat amount, or non-habitat in a landscape-extent circle surrounding a patch were the best measures of patch isolation (Bender et al. 2003, Tischendorf et al. 2003). For ovenbird, we found that amount of habitat at the 300 m and 2000 m extents were important predictors of occurrence and reoccurrence. Small patches in landscapes with low amounts of suitable habitat were less likely to be occupied. In landscapes with high proportions of suitable habitat, ovenbird movement is unlikely to be restricted by the small gaps that occur. However, as the proportion of suitable habitat declines, gaps between patches become greater and emerge as potential barriers to moving adults and juveniles (Hinsley 2000). Indeed, previous research in a forest mosaic indicates that this species may avoid crossing gaps during the breeding season (Robichaud et al. 2002, Bayne et al. 2005) and is less likely to move through landscapes with low forest cover (Belisle et al. 2001, Gobeil and Villard 2002).

Ovenbirds are ground nesters and foragers that rely on invertebrates found in deciduous litter (Burke and Nol 1998). This specialization may require dispersal or extra-territorial movements through a narrow range of forest types; if the species moves preferentially through what we defined as ovenbird habitat, connected patches will be used more frequently in landscapes with low proportions of suitable habitat.

Our spatial autocorrelation analysis indicates that responses to landscape structure by this species may be driven by a tendency to aggregate. Even after controlling for the effects of local vegetation, ovenbird tended to be positively autocorrelated at 350 m (occurrence 2002, 2003) and 700 m scales (occurrence 2002, 2003, reoccurrence); clustering seems to occur independent of local habitat structure. Models including landscape terms were not autocorrelated. Landscape pattern thus seems to account for the observed aggregation in this species. Forest birds have been shown to rely on cues from conspecifics (Danchin et al. 2004) or heterospecifics (Mönkkönen et al. 1999) for information about habitat quality. Small, isolated patches would be less likely to contain large numbers of cue-providing individuals, reducing the opportunity to capitalize on social information (Danchin et al. 2004) and thus decreasing settlement rates. Isolation effects could also result from reduced opportunities for extra-pair fertilization in birds– an occurrence that is potentially much more common than previously assumed (Chuang-Dobbs et al. 2001, Webster et al. 2001) and may boost productivity (Holmes et al. 1992). Presumably, it is more risky to foray into patches at greater distances, as it requires more energy and longer periods away from defended territories (Woolfenden et al. 2005).

For blackburnian warbler, the variables representing the amount of poor-quality matrix at both spatial extents were the most important predictors. Forest types that are clearly non-habitat ($\hat{p}$ <0.05) may constitute barriers to this species (Belisle et al. 2001). Avoidance of landscapes with poor-quality matrix could reflect either supplementation behaviour by this species, or restricted movement of juveniles. This result for blackburnian warbler supports previous research indicating that the landscape matrix quality can influence species movement and distributions (Lindenmayer et al. 2002, Brotons et al. 2003, Baum et al. 2004, Tubelis et al. 2004).

Why did we detect a patch size effect for ovenbird but not blackburnian warbler? Because our initial habitat model for blackburnian warbler had lower prediction success than the ovenbird model, it is possible that we did not define patches as effectively. However, we situated sample points in patches where the distinction between habitat and non-habitat was the least ambiguous (see *Methods*). This reduced the likelihood that areas beyond defined patch boundaries were still adequate habitat. Alternatively, differences may be due to foraging breadths of these species. Blackburnian warblers have specialized nesting requirements, but a broader foraging niche than ovenbirds (Morse 1994). This may allow movement through a wider range of forest types, resulting in a more permeable matrix (McComb 1999). For instance, Vega et al. (1998) found that juvenile wood thrushes (*Hylocichla mustelina*) tended to disperse where food availability was high, rather than remaining solely in mature deciduous forest that characterizes natal territories.

Conservation implications

Our most important management-related finding is that habitat loss is unlikely to result in a proportional decline in the number of animals. For both species, landscape composition is an important predictor of occurrence and reoccurrence. For ovenbird, landscape configuration is also important. If timber harvesting creates high amounts of low quality matrix for blackburnian warblers, population decline will occur more rapidly than expected from simple loss of habitat.

For this species, enhancing the permeability of the landscape matrix may increase occurrence in sites with appropriate local scale habitat.

Our finding that the probability of ovenbird occurrence is greater in larger patches, but only in landscapes with low proportions of suitable habitat, suggests that manipulating landscape pattern (e.g., leaving some large patches unharvested) may mitigate the negative effects of habitat loss for some species. This is particularly important in light of current declines in mature forest in New Brunswick due to timber harvesting (Betts et al. 2003). However, altering the spatial configuration of blackburnian warbler habitat is unlikely to have beneficial results. Further, non-linear fragmentation effects are probably context specific; it is possible that as the amount of suitable habitat at a broader regional scale declines, interactions between landscape configuration and composition could shift. This hypothesis may be tested through simulation (e.g., Donovan and Thompson 2001, Larson et al. 2004); it is usually untenable to manipulate habitat amount experimentally at such large scales. However, an organism-based approach applied to multiple species may offer the opportunity to test this hypothesis empirically since each species simultaneously perceives the region as containing different proportions of suitable habitat. Species with similar degrees of habitat specialization to ovenbird should exhibit greater responses to landscape pattern if there is less suitable habitat at the regional scale.

That the majority of variance in the occurrence of both species was explained by composition variables at the local and landscape scale gives support to the basic premise that maintaining the amount of habitat in the landscape is critical. However, our observation of a non-linear fragmentation effect for ovenbird further suggests that managers can justifiably pay attention to landscape configuration effects to further enhance the conservation value of landscapes for some species.

Acknowledgments

We are grateful to A. Breton, S. Makepeace, J. Nocera, N. Simon, two anonymous reviewers, and J. Marzluff who provided useful comments on this manuscript. Also, thanks are due to J. Cormier, A. Frank, G. George, A. Hadley, R. Kuzyk, D. Mitchell, K. Pistak, A. Whaley, E. Widden, and B. Zitske who assisted in the field component of this study, and to S. White and R. Taylor who assisted in compilation of GIS data. Financial support was provided by the New Brunswick Environmental Trust Fund, New Brunswick Department of Natural Resources, the Fundy Model Forest, Fundy National Park, and a doctoral fellowship to MGB from the Natural Sciences and Engineering Research Council (NSERC). This is ACWERN publication No. UNB-49.

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Tables

TABLE 1. Correlation (*r*) among landscape configuration and composition variables for blackburnian warbler (bold below diagonal), and ovenbird (italics, above diagonal) (*N*=363).

	HAB300	HAB2000	MATRIX300	MATRIX2000	Patch†	Edge††
HAB300	1.00	*0.50*	*-0.65*	*-0.34*	*0.71*	*0.42*
HAB2000	**0.64**	1.00	*-0.31*	*-0.80*	*0.55*	*0.21*
MATRIX300	**-0.70**	**-0.44**	1.00	*0.41*	*-0.50*	*-0.49*
MATRIX2000	**-0.42**	**-0.84**	**0.47**	1.00	*-0.44*	*-0.31*
Patch	**0.71**	**0.57**	**-0.54**	**-0.48**	1.00	*0.37*
Edge	**0.40**	**0.31**	**-0.52**	**-0.37**	**0.32**	1.00

Notes: HAB = Habitat. This was calculated as the summed estimated probability of occurrence for both species ($\hat{p}$) for all 30 m^2 pixels within a 300 or 2000 m radius. MATRIX = Amount of non-habitat ($\hat{p}$ <0.05) within a 300 or 2000 m radius. See *Methods* for details. Numbers beside variable names indicate spatial extent of variables (the radius of a circle centered on each sample point).

†Patch size

††Distance to hard edge

TABLE 2. Coefficients (β) and lower (LCI) and upper (UCI) 95% confidence intervals for blackburnian warbler Generalized Linear Mixed Models with the lowest AIC in 2002, 2003 and for reoccurrence.

Variable	2002			2003			Reoccurrence		
	β	LCI	UCI	β	LCI	UCI	β	LCI	UCI
Intercept	0.672			-0.266			1.065		
Trees>30	0.205	0.051	0.359	0.286	0.127	0.445	0.303	0.129	0.478
Canopy cover (%)	0.665	-0.250	1.580	-	-	-	-	-	-
HWD>10	-0.242	-0.488	0.004	-0.142	-0.396	0.111	-0.494	-0.812	-0.176
SWD>20	-0.177	-0.263	-0.090	-0.123	-0.215	-0.032	-0.235	-0.357	-0.112
MATRIX300	-0.005	-0.009	-0.001	-0.005	-0.010	-0.001	-0.005	-0.011	0.000
MATRIX2000	-0.0001	-0.0003	0.0000	-	-	-	-0.0001	-0.0003	0.0000
HWD>10 * SWD>20	0.052	0.031	0.074	0.041	0.019	0.063	0.067	0.038	0.096

Notes: Trees>30 = number of trees >30 cm dbh/ ha, HWD>10 = number of hardwood trees >10 cm dbh/ ha, SWD>20 = number of softwood trees >20 cm dbh within a 50 m radius. For other abbreviations see Table 1.

TABLE 3. Akaike weights (w_i), evidence ratios (Evidence), and number of parameters (K) from AIC-based model selection for blackburnian warbler occurrence in 2002, 2003 and for reoccurrence.

Hypothesis	2002			2003			Reoccurrence		
	w_i	Evidence	K	w_i	Evidence	K	w_i	Evidence	K
Random sample	0.00	169.7	6	0.03	11.9	5	0.01	40.0	5
Composition	**0.22**	1.0	8	**0.39**	1.0	6	**0.30**	1.0	7
Fragmentation	0.03	6.8	8	0.06	7.0	8	0.05	6.2	7
Non-linear fragmentation	0.03	7.0	9	0.01	38.1	8	0.02	16.8	8

Notes: Only models with the lowest AIC for each landscape hypothesis are shown. All models within a year and for reoccurrence contain the same local-scale variables. Weights of models with the greatest support given the data are highlighted.

TABLE 4. Coefficients (β) and lower (LCI) and upper (UCI) 95% confidence intervals for ovenbird Generalized Linear Mixed Models with the lowest AIC in 2002, 2003 and for reoccurrence.

Variable	2002			2003			Reoccurrence		
	β	LCI	UCI	β	LCI	UCI	β	LCI	UCI
Intercept	-7.338			-4.026			-5.927		
Hardwood BA	0.035	0.008	0.062	0.030	0.008	0.052	0.029	0.007	0.051
Litter (%)	1.561	0.497	2.625	-	-	-	0.610	0.065	1.286
Canopy cover (%)	0.943	0.195	1.691	0.851	-0.052	1.754	1.061	0.116	2.006
OVEN300	0.011	0.004	0.018	-	-	-	-	-	-
OVEN2000	0.0007	0.0003	0.0011	0.0004	0.0001	0.0007	0.0006	0.0002	0.0009
Patch size (ha)†	1.745	0.644	2.846	1.156	0.358	1.954	1.620	0.684	2.557
OVEN2000 * Patch size	-0.0005	-0.0003	-0.0002	-0.0002	-0.0003	-0.00005	-0.0003	-0.0004	-0.0001

Notes: Hardwood BA = hardwood basal area/ ha (m^2). For other variable abbreviations see Table 1.

†Log transformed.

1

TABLE 5. Akaike weights (w_i), evidence ratios (Evidence), and number of parameters (K) from AIC-based model selection for ovenbird occurrence in 2002, 2003 and for reoccurrence.

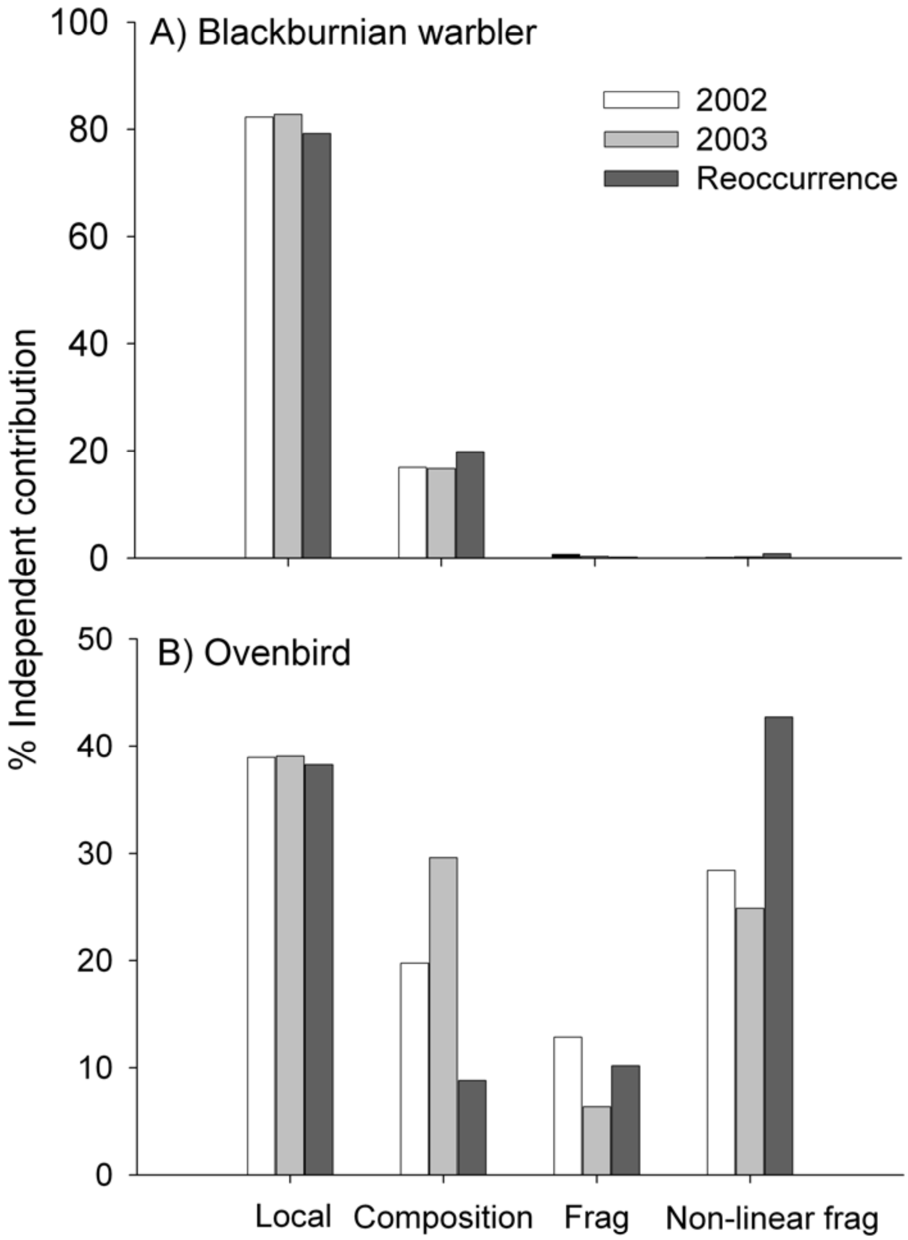
Hypothesis	2002			2003			Reoccurrence		
	w_i	Evidence	K	w_i	Evidence	K	w_i	Evidence	K
Random sample	0.00	$2.89*10^4$	4	0.03	6.66	3	0.02	30.72	4
Composition	0.01	66.06	5	0.18	1.03	4	0.02	26.03	5
Fragmentation	0.00	274.55	7	0.03	6.16	6	0.01	75.04	6
Non-linear fragmentation	**0.89**	1.00	8	**0.20**	1.00	6	**0.55**	1.00	7

Notes: Only models with the lowest AIC for each landscape hypothesis are shown. All models within a year and for reoccurrence contain the same local-scale variables. Weights of models with the greatest support given the data are highlighted.

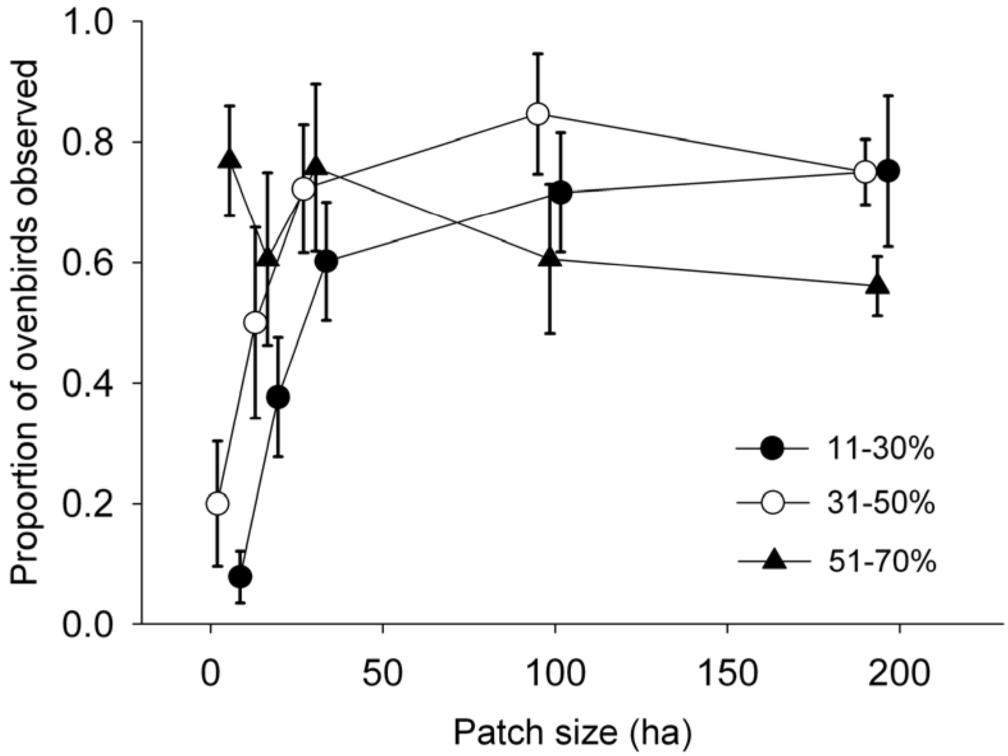
Figure Captions

FIG. 1. Variance partitioning results showing the proportion of independently explained variance by local-scale, landscape composition, landscape fragmentation, and non-linear fragmentation (Non-linear frag) variables for blackburnian warbler (A) and ovenbird (B) in 2002, 2003 and for reoccurrence.

FIG. 2. Interaction between effect of patch size and landscape extent habitat amount (% within a 2000 m radius) on the raw proportion (±SE) of ovenbirds observed in 2002. For graphical purposes, proportions were calculated from the ratio of presences to absences within five categories: 0-5 ha, 6-20 ha, 21-50 ha, 51-100 ha, >100 ha and three habitat amount categories (above). SE was calculated as $\sqrt{(p * q)/N}$ where p = proportion of presences in a category, and q = the proportion of absences. Proportions do not control for local site variation as was conducted in statistical models.



A) Blackburnian warbler
2002
2003
Reoccurrence
% Independent contribution
B) Ovenbird
Local
Composition
Frag
Non-linear frag
100
80
60
40
20
0
50
40
30
20
10
0


Proportion of ovenbirds observed
1.0
0.8
0.6
0.4
0.2
0.0
0
50
100
150
200
Patch size (ha)
11-30%
31-50%
51-70%

APPENDIX A

A table showing local and landscape variables used to predict build models to predict the occurrence and reoccurrence of blackburnian warbler and ovenbird are available in ESA's Electronic Data Archive: *Ecological Archives*.

APPENDIX B

AIC model rankings, weights (w_i) and evidence ratios (ER) of blackburnian warbler models for 2002 are available in ESA's Electronic Data Archive: *Ecological Archives*.

APPENDIX C

AIC model rankings, weights (w_i) and evidence ratios (ER) of blackburnian warbler models for 2003 are available in ESA's Electronic Data Archive: *Ecological Archives*.

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APPENDIX D

AIC model rankings, weights (w_i) and evidence ratios (ER) of blackburnian warbler models for reoccurrence are available in ESA's Electronic Data Archive: *Ecological Archives*.

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APPENDIX E

AIC model rankings, weights (w_i) and evidence ratios (ER) of ovenbird models for 2002 are available in ESA's Electronic Data Archive: *Ecological Archives*.

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APPENDIX F

AIC model rankings, weights (w_i) and evidence ratios (ER) of ovenbird models for 2003 are available in ESA's Electronic Data Archive: *Ecological Archives*.

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APPENDIX G

AIC model rankings, weights (w_i) and evidence ratios (ER) of ovenbird reoccurrence models are available in ESA's Electronic Data Archive: *Ecological Archives*.