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Effects of landscape composition and configuration on northern flying squirrels in a forest mosaic

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ABSTRACT

Habitat loss and sometimes habitat fragmentation *per se* affect species survival, reproduction, dispersal, abundance and distribution. However, understanding the independent effects of fragmentation (i.e., landscape configuration) has been limited because it is frequently confounded with landscape composition (i.e., habitat amount). We assess the independent effects of landscape composition and configuration on the occurrence of northern flying squirrels (*Glaucomys sabrinus*) in New Brunswick, Canada after controlling for local site conditions. We measured landscape structure using an “organism-based” approach; landscape structure was characterized quantitatively using a spatially explicit local-scale distribution model for northern flying squirrels.

Flying squirrels occurred more frequently in old forest, at sites with mixed coniferous–deciduous microhabitat composition and greater amounts of habitat cover at the neighbourhood (within home-range) scale. Squirrels were less likely to occur at sites surrounded by greater proportions of non-habitat matrix (non-treed or early seral open areas). The occurrence of flying squirrels was not strongly correlated with patch size or edge contrast. We detected no interaction between the effects of patch size and habitat composition. Landscape composition was clearly a more important predictor of flying squirrel distribution than configuration. We conclude that management practices that maximize the amount of old forest cover, maintain diverse tree species composition and minimize the creation of open areas should enhance the conservation value of landscapes for northern flying squirrels. Manipulating landscape pattern through forest management likely has limited use in mitigating the negative influence of habitat loss on this species.

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1. Introduction

Habitat loss and fragmentation have been identified as primary threats to the global loss of biodiversity (Pimm et al., 1995; Schipper et al., 2008). These two important components of landscape structure interact across broad spatial scales, making it difficult to identify the cause of population responses. Landscape composition includes the amount and type of landscape elements, while landscape configuration describes their spatial arrangement. Organisms may be affected by both landscape composition and configuration (Turner, 1989), but to different degrees (Fahrig,

1997; Villard et al., 1999; Wiegand et al., 2005). Changes in landscape configuration may lead to habitat fragmentation, the subdivision of contiguous habitat into smaller, more isolated patches. The effects of habitat loss and fragmentation are often confounded in non-experimental, natural landscapes because habitat loss is typically the process by which fragmentation occurs. Assessing the independent effects of landscape structural components is important because configuration can be manipulated independent of habitat amount, potentially allowing managers to minimize the effects of habitat loss or degradation on populations.

Most studies fail to control for the amount of habitat while assessing the effects of landscape configuration (Fahrig, 2003). Of those studies controlling for the amount of habitat, several conclude that landscape composition has a far greater effect on wildlife populations than the negligible influence of landscape configuration (Trzcinski et al., 1999; Heikkinen et al., 2004), supporting the *landscape composition hypothesis* (Fahrig, 2003).

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However, the nature of this relationship remains controversial and varies according to species' attributes (e.g., Villard et al., 1999).

Some species may respond consistently to landscape configuration despite varying landscape composition (*landscape configuration hypothesis*, Villard et al., 1999; Betts et al., 2006). Changes in landscape configuration may reduce the probability of population persistence if the dispersal ability of individuals is disrupted (Bélisle et al., 2001; Banks et al., 2005) or through indirect mechanisms such as the spatial distribution of predators. Small patches may attract disproportionately fewer individuals than large patches for species using conspecifics in habitat selection (Fletcher, 2006). Large patches may provide a source of dispersing individuals within metapopulations, while networks of smaller patches may allow persistence through the asynchrony of local population dynamics (Hanski, 1998). The *landscape configuration hypothesis* suggests that species respond to landscape configuration independent of landscape composition.

Animals may alter their response to landscape configuration in the presence of varying landscape composition, responding to landscape configuration only once the amount of habitat in the surrounding landscape drops below some threshold amount (Andrén, 1994). There is both theoretical (With and Crist, 1995; Bascompte and Solé, 1996) and empirical (Jansson and Angelstam, 1999; Radford et al., 2005; Betts et al., 2007) support for this *fragmentation threshold hypothesis*, which suggests that the effects of landscape composition and configuration become multiplicative as habitat becomes increasingly rare within the surrounding landscape.

Research on the response of various taxa to fragmentation in forest mosaics has been susceptible to several challenges. First, studies failing to control for local site characteristics may misinterpret responses to local conditions as responses to landscape structure (Heikkinen et al., 2004) due to high inter-site variation in many forested landscapes. Testing variables at multiple spatial extents and resolutions is important for both improved species occurrence models and for making forest management recommendations, as species are influenced by composition and structure at multiple spatial scales (Wiens, 1989). Second, it is essential to appropriately define the distribution of habitat for the species in question (i.e., an organism-based approach; Betts et al., 2006). Researchers have tended to rely on generic qualitative definitions of land cover (e.g., 'forest' Trzcinski et al., 1999). Though this may be appropriate in landscapes where boundaries between patches and matrix are clear (e.g., islands, forest-agricultural mosaics), it likely alters the power to detect landscape effects in forest mosaics (Betts and Villard, 2009) where ecotone gradients are more common than sharp boundaries and patch delineation is ambiguous (Mönkkönen and Reunanen, 1999).

Our objective was to test for the independent effects of landscape composition and configuration on northern flying squirrel (*Glaucomys sabrinus*) occurrence while assessing and controlling for microhabitat and local habitat associations. This arboreal species is reliant on old forest characteristics, is considered a forest keystone species (reviewed in Smith, 2007) and has been proposed as a forest management indicator species. The species' habitat associations, locomotion and general biology suggest that it may be particularly sensitive to landscape configuration (Carey, 2000; D'Eon et al., 2002; Scheibe et al., 2006; Smith and Person, 2007), however no previous study has assessed its response to landscape structure while controlling for the confounding effects of landscape composition and variation caused by site-scale habitat quality.

2. Materials and methods

Our study occurred within the Greater Fundy Ecosystem of southern New Brunswick, Canada (66.08°W–64.96°E, 46.08°N–

45.47°S, ~360 km²). This region is characterized by a maritime climate, rolling topography (elevation 70–398 m) and is a forest mosaic of unmanaged and actively managed coniferous (30% total with 7% plantations), deciduous (25%) and mixed coniferous–deciduous (27%) stands. Coniferous areas are dominated by red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*), with an abundance of snags resulting from a spruce budworm (*Choristoneura fumiferana*) epizootic in the 1970s. Deciduous tree species include white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), sugar maple (*Acer saccharum*), yellow birch (*B. alleghaniensis*), red maple (*A. rubrum*) and American beech (*Fagus grandifolia*). Clear-cutting, planting and thinning of coniferous stands have been prevalent management activities in the region since the 1970s. Approximately 42% of the study region is covered by old forest (>70 years), 20% by early seral stages (<20 years) and 16% is open, non-treed land.

We trapped for flying squirrels at 53 population monitoring study sites selected using a stratified design to sample the degree of forest alteration, stand age and species composition across a coniferous–deciduous species gradient. At each study site we established a single 'trapline' consisting of two parallel transects separated by 40 m; traps within each transect were spaced at 30 m intervals. We used small trapping grids to enable us to more easily fit them within a single stand type. This was done to reduce within-site variation caused by crossing stand edges. Traps were securely tied to moderate sized trees (10–20 cm diameter at breast height) at a height of approximately 1.25 m and baited with apple wedges and peanut butter. Twenty-five live traps (Model 102, Tomahawk Live Trap Company, Tomahawk, USA) were set within each trapline, which was then trapped for four nights from May to early September 2001. We use traplines ($n = 53$) as our sampling unit during all subsequent analyses, which we summarize as a flow diagram in Fig. 1.

2.1. Microhabitat characterization

We sampled 10 m × 20 m vegetation plots at each study site to characterize microhabitat conditions (e.g., vegetation structure and composition). Plots were centred on three randomly selected traps within each trapline. We recorded the abundance, diameter at breast height (dbh) and species composition of living and dead woody stems, the relative abundance of coarse woody debris and the slope of the terrain; data that are not directly available in the provincial forest inventory (Table 1). We calculated the density per plot of coniferous trees >10 cm dbh, deciduous trees >20 cm dbh and snags >10 cm dbh (Gerrow, 1996). We also recorded the slope of the terrain and the relative abundance of coarse woody debris. These measures were averaged across the three sampling plots to determine trapline values.

2.2. Local site characterization

We used the coarse resolution data available in the New Brunswick provincial forest inventory to calculate the amount of old ("stable or declining volume", >70 years old), coniferous (>75% coniferous tree species in dominant layer) and mixedwood (<75% coniferous and <75% deciduous tree species in dominant layer, Timber Management Branch, 1986) forest cover within a 2.6 ha area (91 m radius) surrounding the centre of each study site. This extent approximates the core usage area of a female northern flying squirrel within the study area (Gerrow, 1996; also see Smith, 2007). We also assessed the effects of canopy cover (classified as either greater or less than 50% closure), elevation, slope and the distance to the nearest stream. Extensive research on northern flying squirrels suggests species distribution is affected by tree species composition, the availability of legacy structures (e.g.,

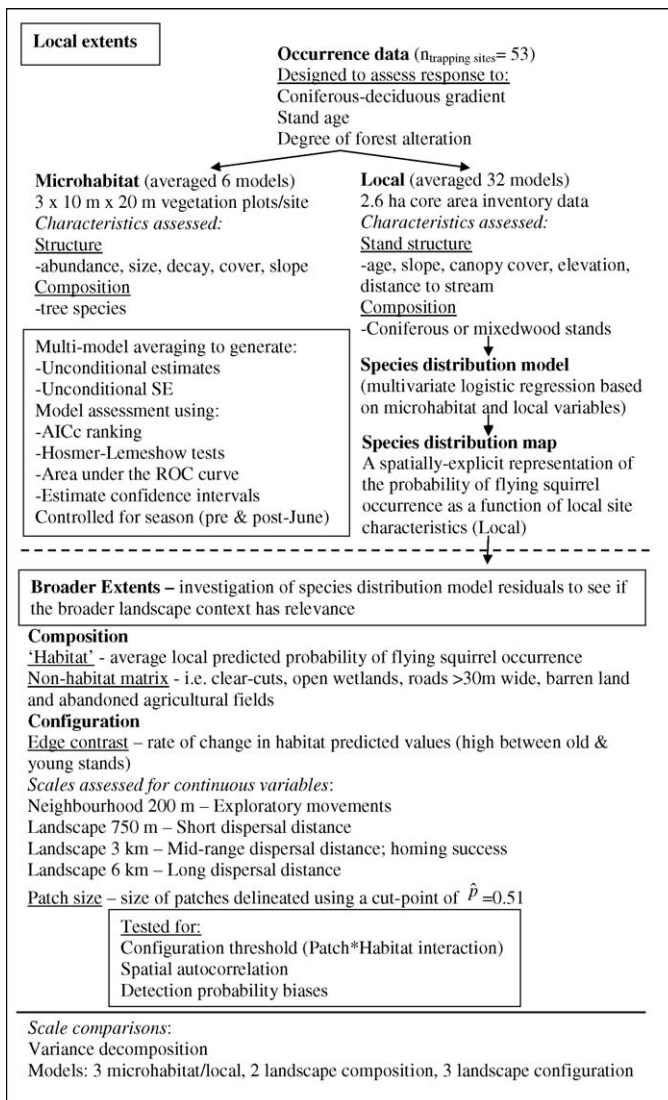


Fig. 1. Diagram of study design including an overview of response (occurrence data), predictor variables and analyses conducted at each scale. ROC: Receiver Operating Characteristic.

snags, coarse woody debris), the amount of canopy cover and the distance to streams in drier forests (summarized in Smith, 2007; Weigl, 2007). Spatial forest inventory data are derived from digitized aerial photographs (1993, 1:12,500 scale, colour). The data are at least 80% representative of forest cover as verified by on-the-ground sampling (Province of New Brunswick unpublished data). The presence of recent clear-cuts was updated using the most recently available satellite imagery (Betts et al., 2003).

2.3. Statistical approaches: Microhabitat

We used preliminary univariate assessments of the response of flying squirrels to their immediate site conditions to screen microhabitat candidate variables. Variables with standard deviations larger than their parameter estimates were eliminated. We chose this criterion for variable selection because: (1) variables important in a multivariate context are more likely to be retained when liberal cut-offs are used (Underwood, 2001) and the risk of over-fitting models can be mitigated by careful *a priori* variable consideration; (2) if the variability of a maximum likelihood estimate is greater than the estimate itself, there is little chance of it being useful as a predictor.

We evaluated species response to the density of snags >10 cm dbh, for all trees >20 cm dbh, deciduous trees >20 cm dbh, coniferous trees >10 cm dbh and for a statistical interaction between the two latter variables (indicating a mixedwood association; Young et al., 2005). We also assessed the effect of coarse woody debris abundance, slope of the terrain, and elevation.

This process of variable elimination resulted in a candidate set of 6 models. We used Akaike’s Information Criterion modified for small sample size (AICc) in model selection. We adopted a model-averaging strategy (Burnham and Anderson, 2002); we calculated unconditional parameter estimates and standard errors to incorporate model uncertainty (Burnham and Anderson, 2002; SAS Institute Inc., 2002; Shaffer, 2004). We then tested for goodness-of-fit using Hosmer–Lemeshow tests and by determining the area under the Receiver Operating Characteristic Curve (AUC, Hosmer and Lemeshow, 2000; Vida, 2001). AUC, which ranges from 0.5 (random prediction success) to 1 (perfect prediction success), quantifies the ability of a model to correctly classify observations into one of two possible outcomes based on model sensitivity (the number of observations correctly classified as positive) and specificity (the number of observations incorrectly classified as positive).

2.4. Species distribution model

Using an organism-based approach first requires a quantitative estimate of the spatial distribution of habitat for a species at local scales (e.g., Elith et al., 2006; Betts et al., 2007). Species distribution models are then used to characterize the landscape structure from a ‘species-eye’ view (see Sections 2.5 and 2.6). We used the occurrence of flying squirrels to derive a species distribution model using multivariate logistic regression and local-scale forest inventory data. Prior to building this model, we graphically assessed the distribution, the degree of correlation and the amount of shared and independently explained deviance of each candidate variable. Using the approach outlined for microhabitat above, we conducted a preliminary univariate assessment of the response of flying squirrels to local site conditions. This variable elimination process resulted in a candidate set of 32 models. Once again, we used a same multi-model-averaging strategy to derive robust local-scale parameter estimates.

We mapped our distribution model using Spatial Analyst in ArcView 3.3 (Environmental Systems Research Institute Inc., 2002, Redlands, USA). These predicted values thus represent the probability of flying squirrel occurrence as a function of local habitat characteristics (‘Local’, Fig. 2). The residuals of the local model were then investigated to see if flying squirrels respond to the broader landscape context. Because only local variables were used to develop our distribution model, the analyses described below assess whether landscape characteristics help to predict flying squirrel occurrence *after* accounting for local site conditions.

2.5. Landscape composition

We assessed the response of flying squirrels to habitat amount at four ‘landscape’ spatial extents. We selected these extents to represent exploratory movements (neighbourhood scale, 200 m radius; Gerrow, 1996), short-distance dispersal events (750 m radius; estimated from *Pteromys volans*: Selonen and Hanski, 2003), mid-range dispersal and homing success (3 km radius; Selonen and Hanski, 2004; Bourgeois, 1997 respectively) and long-distance dispersal movements (6 km radius; Carey, 2000; Bowman et al., 2002; Smith, 2007). We calculated an index of habitat amount by averaging the predicted values of the species distribution model (\hat{p} ; hereafter ‘habitat amount’ or Habitat)

Table 1

Microhabitat, local and landscape structure predictors of northern flying squirrel (*G. sabrinus*) occurrence, with two resolutions for local data. Forest inventory data were used to build the species distribution model.

Variables	Variable description	Mean ± SD
Deciduous*Coniferous	Proportion of mixedwood stands within a 91 m radius ⁱ Interaction between avg. density of deciduous trees >20 cm dbh and density of coniferous trees >10 cm dbh per 200 m ^{2v}	Conifers: 12.4 ± 14.6 Deciduous: 3.2 ± 2.4
Old forest cover	Stand areas with stable or declining wood volume (91 m radius) ⁱ	0.60 ± 0.46
Canopy cover	Canopy cover (categorical, 0: <50%, 1: >50%) ⁱ Avg. canopy cover along plot perimeter ^v	77% of sites in category 1
Distance to stream /moisture	Distance to nearest stream (m) ⁱ	350 ± 262
Slope	Slope of terrain (in degrees) ⁱ Avg. slope of terrain at trapping location ^v	8 ± 6
Elevation	Elevation (in m) ⁱ	223 ± 108
Snags	Average density of snags >10 cm dbh at site ^v	4.0 ± 2.5
Cwd	Number of logs >8 cm dbh along a 20 m transect ^v	
'Habitat' (12.6 ha)	Avg. probability of flying squirrel presence within surrounding area	0.46 ± 0.21
Edge contrast	Avg. slope of flying squirrel occurrence probabilities within a given radius	0.076 ± 0.011
Matrix (176 ha)	Proportion of non-habitat matrix (e.g., open, non-forested area)	0.12 ± 0.09
Patch	(log ₁₀ + 1) transformed patch area ($N_{\text{unique}} = 14, N_{\text{not in patch}} = 28$)	1630 ± 2830 ha ^{raw data}

^v microhabitat data.

ⁱ local-scale provincial forest inventory data.

within a given radius surrounding the trapline centre (after Betts et al., 2006, 2007). We also calculated the amount of non-treed, open area (i.e., clear-cuts, open wetlands, wide roads >30 m, barren land and abandoned agricultural fields) in the surrounding

landscape, which we designated as non-habitat 'Matrix' based on (1) the low probability of occurrence ($\hat{p} < 0.05$) in our species distribution model, (2) the general ecology of flying squirrels (Smith, 2007) and (3) the energetic efficiencies of gliding locomotion (Scheibe et al., 2006). When the correlation between variables was greater than 0.6, we retained only the variable with the smallest residual deviance and eliminated any variable that explained little additional deviance (<10% total explained deviance, Chevan and Sutherland, 1991; Fletcher and Hutto, 2008).

Because fewer squirrels were caught during our early spring trapping [May ($n = 12$) compared to August ($n = 11$) because only 3 sites were trapped in September, $\beta = -2.20$, SE = 0.99, $\chi^2 p = 0.02$] we analyzed pre- and post-June trapping data separately by including trapping season as a factor in subsequent landscape analyses. The difference between May and June trapping success is consistent with previous research in our study area (e.g., early May 1999: 8.3%; early June 1999: 22.5% in Vernes, 2004).

2.6. Landscape configuration

Although a multitude of methods are available for quantifying landscape configuration (e.g., McGarigal et al., 2002), only a few of these appear to influence species distributions in empirical studies. We selected edge and patch size as configuration variables because there is ecological basis for expecting effects; more than any other measures of fragmentation, meta-analyses and reviews have revealed the biological importance of these metrics in a range of contexts (Bender et al., 1998; Fagan et al., 1999; Lidicker, 1999).

We quantified edge contrast as the spatial rate of change in \hat{p} within the landscape surrounding the centre of each trapline. High edge contrast occurs in areas of juxtaposition between high and low \hat{p} ; for example, high juxtaposition often occurred at the boundary between old and young forest stands. Low edge contrast occurs in regions with more uniform conditions (e.g., between locations of similar forest stand age). We tested the response of flying squirrels to edge contrast at the same four spatial extents described above.

Although treating landscapes as continua is preferential to a binary description (Fischer and Lindenmayer, 2006), the concept of a "patch" requires the presence of boundaries. To classify our study areas into patches, we had to identify a single cut-point between

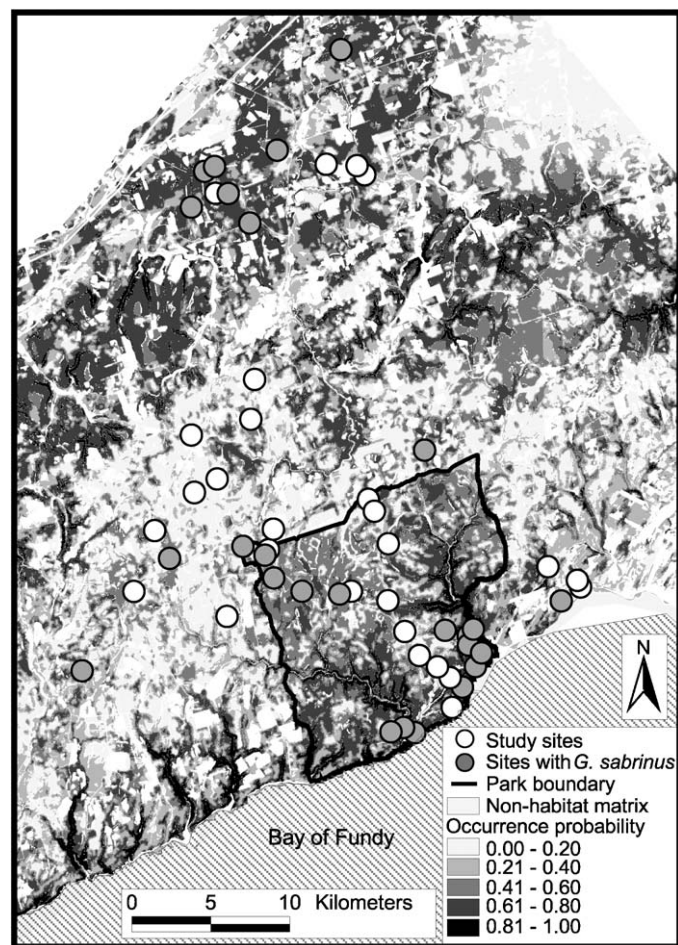


Fig. 2. Northern flying squirrel (*Glaucomys sabrinus*) trapline locations overlaid on a map of local species distribution derived from provincial forest inventory data.

flying habitat and matrix. The Receiver Operating Characteristic (ROC) curve describes signal-detection in the presence of noise by displaying the trade-offs between true (sensitivity) and false (1-specificity) signals (Hosmer and Lemeshow, 2000). We quantitatively established patch boundaries from our species distribution model. We did so using thresholds in the ROC to determine a cut-point in \hat{p} that maximized model prediction success by simultaneously maximizing model sensitivity (the proportion of occurrences correctly predicted) and specificity (the proportion of absences correctly predicted, Hosmer and Lemeshow, 2000). ROC assesses model performance across the full range of threshold values, therefore our cut-point for delineating boundaries between patch and matrix was informed by the frequency of flying squirrel occurrence ($\hat{p} = 0.51$, Manel et al., 2001; Guénette and Villard, 2005). We $\log_{10}(x + 1)$ transformed the size of the resulting patches prior to analysis.

To test the *landscape composition*, *landscape configuration*, and *fragmentation threshold* hypotheses, we adopted the following model selection strategy. First, to control for the effect of local-scale variation, we included the fitted values from Microhabitat and Local-scale variables into all models. Similarly, all tests for landscape configuration effects (i.e., patch size, edge contrast) statistically controlled for the effects of landscape composition (Fahrig, 2003). We determined if the effect of landscape configuration varies with habitat amount at the landscape scale by testing for an interaction between measures of landscape composition and configuration (i.e., the *fragmentation threshold hypothesis*; Trzcinski et al., 1999). Our final candidate model set contained 8 models representing only the effects of microhabitat and/or local habitat (3 models), as well as those including landscape composition (2 models), and landscape configuration (3 models). We do not report averaged model coefficients for landscape analyses because our interest was in hypothesis testing rather than prediction (Burnham and Anderson, 2002). We compared the relative independent (unique) and total variance explained by each component of our final model and for landscape configuration metrics (edge contrast and patch size) using a variance decomposition approach (Chevan and Sutherland, 1991; Fletcher and Hutto, 2008).

It is important to note that, though our study area is primarily forested, there is a large gradient in the degree of fragmentation and the amount of old forest at landscape scales. Old forest cover, the most influential predictor for our species distribution model (see Section 3), varied from 2% to 99% (mean: 44%, SD: 22%) within the surrounding landscape (176.7 ha). The amount of non-habitat Matrix at the same scale ranged from 0% to 36% (mean: 12%, SD: 9). These variables were not significantly correlated ($r = -0.08$, $df = 51$, $p = 0.57$). Edge Contrast at a 3 km radius ranged from 0.042 to 0.091 (mean: 0.076, SD: 0.011). Measures of Patch size, Edge Contrast and Habitat amount were not strongly correlated ($r_{\text{Habitat-Patch}} = -0.095$, $r_{\text{Habitat-Edge Contrast}} = -0.17$, $r_{\text{Edge Contrast-Patch}} = 0.33$). The large fragmentation gradient combined with the lack of confounding among key predictor variables enabled us to successfully test the fragmentation threshold hypothesis.

We tested for spatial autocorrelation to satisfy the assumption of independence of errors (Legendre, 1993). We did so by assessing the Pearson residuals of local and landscape models using Moran's I correlograms following Lichstein et al. (2002), with a lag distances of both 200 and 600 m.

Species distribution models can often be biased by differential detection probability across environmental gradients and seasonal variation. We calculated overall detection probability (p) using the methods of MacKenzie et al. (2002) in PRESENCE software. We also tested for the influence of our most important landscape-extent variable, non-habitat matrix within a 750 m radius (see Section 3)

on p and occupancy (ψ). We tested for differences in flying squirrel occurrence across trapping months (May to September) and controlled for differences prior to testing landscape scale relationships. We conducted statistical analyses in R (R Development Core Team, 2005).

2.7. Variance partitioning

We determined the amount of total, unique and shared variance explained by Microhabitat (200 m²), Local (2.6 ha), neighbourhood ('Habitat'—12.6 ha) and landscape scale ('Matrix'—176 ha, Edge and Patch Size) metrics (Heikkinen et al., 2004; Fletcher and Hutto, 2008). Total variance was derived from univariate models of each predictor. Shared variance, sometimes referred to as joint or confounded variance (Fletcher and Hutto, 2008), is the variation explained by other variables or at different spatial or temporal scales. Unique or conditional variance is the amount of additional variance explained after all other variables in the model are considered.

3. Results

3.1. Microhabitat

We captured flying squirrels at 26 of our 53 sites (49.1%) during 4981 trap-nights (corrected for closures, mean per site: 94.0 ± 5.7 TN, range: 73–100). Flying squirrels were associated with mixed coniferous–deciduous forest composition; we found strong support for an interaction between the density of coniferous and deciduous tree species (Table 2). In our study region, flying squirrels were most likely to occur at mixedwood sites containing at least a 44% coniferous component. This microhabitat model, based on vegetation plot data (log likelihood = -29.6; local = -27.1), had adequate discriminatory power (AUC: 0.73 ± 0.07 SE) and showed no lack of fit (Hosmer–Lemeshow $C = 8.59$, $df = 8$, $p = 0.38$).

3.2. Local species distribution model

Flying squirrels were most frequently found in areas with greater amounts of old forest cover within the surrounding 2.6 ha (β : 2.03, SE: 0.81; Table 3; Fig. 2). The local model containing old forest had excellent discriminatory power (AUC: 0.81 ± 0.06 SE; Hosmer and Lemeshow, 2000; Vida, 2001,) and we detected no lack of fit (Hosmer–Lemeshow $C = 9.15$, $df = 8$, $p = 0.33$). We found no influence of inventory forest type on the occurrence northern flying squirrels.

3.3. Landscape composition

Flying squirrels occurred more frequently in landscapes with more habitat within 200 m (12.6 ha), even after accounting for local conditions; this supports the *landscape composition hypothesis*. Animals also appeared to avoid areas with greater amounts of open, non-habitat matrix within a 750 m radius (176 ha; Tables 4 and 5; $\sum w_i$ for models including both metrics = 0.68). Matrix was present in both of the top models (AIC $\sum w_i = 0.54$). The best model including these landscape variables explained 42.8% of the total deviance and had excellent discrimination power (AUC = 0.89, Hosmer and Lemeshow, 2000).

3.4. Landscape configuration

Flying squirrels within our study region did not appear to be affected by patch size. The landscape model including Patch (β /SE = 0.35) was more than 3 times less likely to be the best model than the same model without this term (evidence ratio = 3.78,

Table 2

Microhabitat associations of northern flying squirrels (*G. sabrinus*) based on microhabitat data, including model-averaged logistic regression coefficients and unconditional standard errors.

Parameter	β_{avg}^*	N_{models}	$SE_{unconditional}^\dagger$	L (90% CL) [‡]	U (90% CL) [§]
Intercept	0.89	6	–	–	–
Slope	0.06	3	0.05	–0.02	0.15
Deciduous (stems/plot)	–0.43	4	0.24	–0.82	–0.05
Deciduous*Coniferous	0.04	2	0.02	0.01	0.08
Coniferous (stems/plot)	–0.08	2	0.04	–0.14	–0.01

Note: Values in bold are parameters with 90% confidence intervals excluding zero.

* β_{avg} : model-averaged coefficient. N_{models} : number of models explicitly including the parameter.

† $SE_{unconditional}$: unconditional standard error estimate.

‡ L (90% CL): lower 90% confidence interval limit.

§ U (90% CL): upper 90% confidence interval limit.

$w_i = 0.10$, Table 4). However, there is some evidence that flying squirrels may negatively respond to sharp edge contrast. The model including Edge Contrast at 3 km ($\beta/SE = -1.12$) was 2 times less likely than the best model, but it remained within $\Delta AICc$ 2 of the top model (evidence ratio = 2.01, $w_i = 0.18$, $\Delta AICc = 1.40$, Table 4). However, 90% confidence intervals around the parameter estimates for Edge Contrast were quite broad ($\beta = -54.48, -134.4, 25.42$). We found little support for the fragmentation threshold hypothesis; there was little statistical support for an interaction between habitat amount and patch size (Habitat*Patch, $\beta/SE = 0.87$, evidence ratio = 10.19, $w_i = 0.04$, Table 4).

A lack of spatial autocorrelation in the residuals of the top landscape model suggests our study sites can be considered spatially independent ($I_{std\ lag\ 200\ m} = -0.38$ to 0.18 , $I_{std\ lag\ 600\ m} = -0.36$ to 0.16 , $\alpha = 0.1$ prior to two-tailed progressive Bonferroni test). On average, the nearest distance between study sites was more than 1.9 km (420–7330 m, SD: 1490, $n = 39$ unique pairings).

3.5. Model bias as a function of detection probability

The probability of squirrel detection for each site visit was high (0.67 ± 0.19 SE), with an overall detection probability across four trap-nights of 0.99 (MacKenzie et al., 2005). We found weak evidence that our most important landscape variable (Matrix) positively influenced detection probability p (ΔAIC 2 from the model with no covariate for p); if flying squirrels occurred at a site, they were more likely to be detected at traplines surrounded by high amounts of non-habitat matrix. However, including estimates of p in models via occupancy modelling did not substantively influence parameter estimates (i.e., β for effects of non-habitat matrix on occurrence = -8.17 , β for effect on ψ : -8.41). Nevertheless, as a result of this small bias, the negative effect of non-habitat matrix on flying squirrel occurrence that we report should be considered slightly conservative.

3.6. Variance partitioning

Our global model including Microhabitat (200 m²), Local (2.60 ha), neighbourhood (Habitat, 12.6 ha) and landscape scale

(Matrix, 176 ha) variables explained 42.8% of the variance. Local measures explained the greatest amount of total explained variance (Microhabitat: 41.9%; Local: 56.5%) and unique explained variance (Microhabitat: 17.3%; Local: 29.7%). However, neighbourhood and landscape scale variables independently contributed to the amount of explained variance (Habitat 200 m: 11.3%; Matrix 750 m: 12.9%, Fig. 3, Table 5). Patch size explained essentially no additional variance after controlling for local and landscape scale composition (0.003% unique explained variance), while edge contrast explained 3.9%.

4. Discussion

4.1. Landscape composition

Flying squirrels responded to their surroundings at a scale larger than within-home-range movements. Our results contribute to a growing body of evidence suggesting that the effects of landscape composition are greater than the independent effects of landscape configuration (McGarigal and McComb, 1995; Fahrig, 2003). These results are consistent with the response of other taxa to landscape composition (e.g., mammals: Kurki et al., 1998; Umetsu et al., 2008; birds: Drapeau et al., 2000; Radford and Bennett, 2007; amphibians: Guerry and Hunter, 2002; Van Buskirk, 2005), although they are scale-dependent and mechanisms for the response likely vary. The incidence of diverse forest bird species was better explained by landscape composition than configuration (e.g., Radford and Bennett, 2007). Tree cover (originally defined as an 'extent' variable but comparable to our definition of landscape composition) and land use (e.g., agricultural enterprise, comparable to non-habitat matrix) were the most prominent explanatory variables for the species assemblage. Similar to ours, the modelling approach used gave priority to composition over configuration. The distribution of forest birds associated with late-seral stand characteristics responded positively to the amount of old-growth forest cover at a landscape scale (Brotons et al., 2003a). Landscape composition may also impose greater constraints on the movements of homing forest birds (Bélisle et al., 2001). It may influence population dynamics through processes such as resource com-

Table 3

Model-averaged coefficients and unconditional standard errors for local-scale logistic regression of northern flying squirrel (*G. sabrinus*) occurrences based on inventory data (also the local species distribution model).

Parameter	β_{avg}^*	$SE_{unconditional}^\dagger$	L (90% CL) [‡]	U (90% CL) [§]
Intercept	–1.22	–	–	–
Canopy cover	0.55	0.76	–0.72	1.81
Elevation	–0.003	0.003	–0.008	0.003
Old forest cover (91 m)	2.03	0.81	0.67	3.39
Slope (inventory)	–0.04	0.06	–0.06	0.15
Distance to stream	–0.001	0.001	–0.002	0.001

Note: Each variable was included in all 32 models. Values in bold are parameters with 90% confidence intervals excluding zero. See Table 2 for explanation of symbols.

Table 4 Parameter estimates (\pm SE), Akaike's Information Criterion (AICc), weights (w_i) and evidence ratios for models of northern flying squirrel (*G. sabrinus*) occurrence across microhabitat (200 m²), local (2.60 ha), neighbourhood (Habitat–12.6 ha) and landscape scales (Matrix–176 ha) while controlling for lower trapping success during May (Season).

Variables	AICc	k	Δ AICc	w_i	Evidence ratio
1.47(1.04)Season + 1.09(0.53)Microhabitat + 1.20(0.44)Local + 12.64(7.28)Habitat – 8.24(4.38)Matrix – 0.037	55.85	6	0.00	0.36	1.00
1.53(1.01)Season + 1.21(0.57)Microhabitat + 1.31(0.45)Local + 13.36(7.64)Habitat – 9.16(4.52)Matrix – 54.48(48.72)Edge + 4.27	57.25	7	1.40	0.18	2.01
1.52(0.92)Season + 1.00(0.49)Microhabitat + 1.14(0.41)Local + 11.97(7.10)Habitat – 1.12	57.34	5	1.49	0.17	2.11
1.59(0.87)Season + 0.90(0.46)Microhabitat + 1.07(0.39)Local – 1.18	58.18	4	2.33	0.11	3.21
1.46(1.06)Season + 1.08(0.54)Microhabitat + 1.18(0.67)Local + 12.59(7.39)Habitat – 8.22(4.42)Matrix + 0.014(0.39)Patch – 0.052	58.51	7	2.66	0.10	3.78
1.71(1.11)Season + 1.19(0.57)Microhabitat + 1.15(0.68)Local + 8.02(8.55)Habitat – 7.48(4.37)Matrix + 0.069(0.41)Patch + 4.29(4.92)Habitat*Patch – 0.36	60.50	8	4.64	0.04	10.19
1.19(0.83)Season + 1.24(0.36)Local – 0.93	60.63	3	4.78	0.03	10.92
1.42(0.77)Season + 1.18(0.40)Microhabitat – 1.07	65.21	3	9.35	0.00	107.45

Table 5

Coefficients (β), standard errors (SE) and explained deviance (null = 73.46) for landscape scale logistic regression of northern flying squirrel (*G. sabrinus*) occurrences using Type I sums of squares to assess the effect of landscape structure after adjusting for local-scale effects.

Parameter	β	SE	Deviance	L (90% CL)	U (90% CL)
Intercept	–0.037	–	Null: 73.46	–	–
Season	1.47	1.04	1.56	–0.27	3.21
Microhabitat (logit)	1.09	0.53	13.18	0.20	1.98
Local (logit)	1.20	0.44	9.37	0.46	1.94
Habitat (within 12.6 ha)	12.64	7.28	3.28	0.43	24.85
Matrix (within 176 ha)	–8.24	4.38	4.04	–15.59	–0.90

plementation and supplementation (Dunning et al., 1992), broad-scale habitat selection (Pulliam and Danielson, 1991), changes in movement efficiency between different cover types (Bélisle et al., 2001; Bender and Fahrig, 2005) and predator–prey interactions (Rodewald and Yahner, 2001).

The negative response of northern flying squirrels to the amount of non-habitat matrix within 176 ha indicates the species responds strongly to landscape context. Habitat loss resulting in patch isolation may alter species distributions (Ficetola, 2004), social interactions (Banks et al., 2005), species richness (Estrada et al., 1994), breeding success (Cooper and Walters, 2002), colonization success (Berggren et al., 2001) and the probability of recolonization (Bélisle et al., 2001). Habitat loss may change movement patterns due to decreased movement efficiency in areas without trees (Scheibe et al., 2006), behavioural changes relating to encountering patch edges (Desrochers et al., 2003), gap-crossing decisions (Bélisle et al., 2001) and/or increased predation risk (Kurki et al., 1998).

Currently, the best indirect measure of isolation effects on colonization, dispersal and patch immigration appears to be the amount of habitat within the surrounding area (Moilanen and Nieminen, 2002; Bender et al., 2003; Tischendorf et al., 2003). The positive response of flying squirrels to high amounts of old forest cover and their apparent avoidance of non-habitat matrix within our study area suggests sensitivity to isolation effects, particularly in areas with very young or no forest cover.

Species' responses to forest cover and open gaps are variable, even for species with similar vagility. For example, red squirrels travelling across unfamiliar ground during homing movements

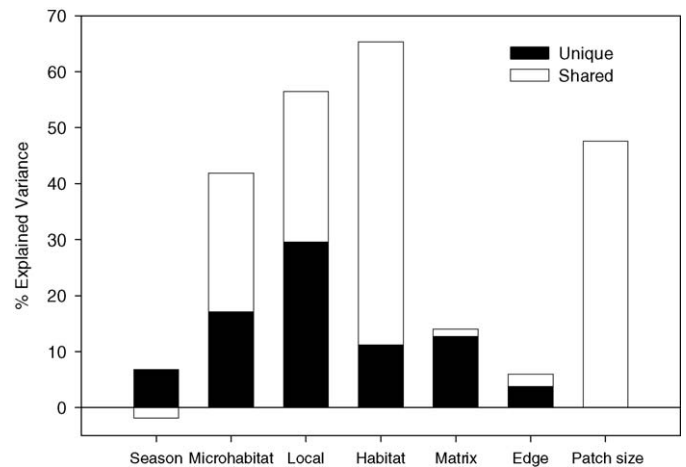


Fig. 3. Unique (conditional) and shared (joint or confounded) explained variance of northern flying squirrel (*G. sabrinus*) capture probability partitioned by microhabitat (200 m²), local (2.6 ha), neighbourhood ('Habitat'–12.6 ha) and landscape scale ('Matrix'–176 ha, Edge and Patch Size) variables. Shared variance suggests the amount of variation that is explained by other variables or different spatial scales.

behaved in a manner suggesting a trade-off between unobstructed movement and reducing the risk of visual detection (Bakker, 2006). Homing individuals detoured around open areas if the detour efficiency was relatively high and they did not have limited energetic reserves (Bakker and Van Vuren, 2004). These results are similar to those reported for homing forest birds (e.g., Bêlisle and Desrochers, 2002). However, Eastern chipmunks (*Tamias striatus*), which are frequently considered to be forest specialists, may experience landscapes with open agricultural areas up to 240 m wide as being functionally connected (Bowman and Fahrig, 2002).

One distinguishing feature between northern flying squirrels and the latter species is their ability to glide, which is energetically more efficient for them than quadrupedal movements (Scheibe et al., 2006). This life-history trait suggests individuals' ability to disperse through open areas may be limited. Smith and Person (2007) found that flying squirrel populations in Alaska were unlikely to be sustained by small, isolated habitat reserves and suggest that dispersal between small reserves will be critical to promote the long-term survival of local metapopulations. Results similar to ours were also reported for Siberian flying squirrels (Reunanen et al., 2004), whose distribution in north-eastern Finland may be largely explained by the amount of open area within a 1 km radius (Mönkkönen et al., 1997). Furthermore, Siberian flying squirrels actively avoid open areas during dispersal movements despite using a variety of stand types and ages for foraging (Selonen and Hanski, 2004).

Even some species capable of flight avoid open areas. Translocated *Scelorchilus rubecula* took longer to move from their release patches if these were surrounded by open matrix (Castellón and Sieving, 2006). Authors suggest that because individuals of this species are poor flyers, the species' response to open matrix may be more akin to those of non-volant species. However, neotropical migrants (Bêlisle and Desrochers, 2002) will detour longer distances within protective forest cover to avoid crossing open gaps.

It may be intuitive to assess species responses to landscape structure based on species' vagility. Functional connectivity depends, at least in part, on the perceptual ability and vagility of the dispersing organism (Zollner, 2000). In a landscape that is structurally fragmented, mobile species that are capable of rapidly traveling long-distances may be able to use a network of patches to move across a landscape despite the patch network itself being physically unconnected. The landscape is functionally connected when organisms are able to disperse between locations. However, the ability and propensity to move through a landscape likely interacts not only with landscape structure but also the species' evolutionary history (Fahrig, 2007) and the individual's state or motivation (Bêlisle, 2005). As such, it may be inappropriate to consider dispersal ability to be a static species-attribute that can be estimated or ranked without considering situational and landscape context.

4.2. Landscape configuration

Flying squirrels within our study area do not show a strong response to landscape configuration as measured by patch size or edge contrast; thus our data do not support the *landscape configuration hypothesis* or the *configuration threshold hypothesis*. The range in the amount of habitat surrounding our study sites suggests we should have been able to detect a threshold response of flying squirrels to landscape composition if one was present (Andrén, 1994). However, we found no support for one. Our study took place in forest mosaic that included fine-grained landscapes with relatively small gaps and graduated boundaries. Research on the Siberian flying squirrel suggests they respond more to landscape configuration in coarse-grained landscapes (Hurme

et al., 2005). The degree of edge contrast in fine-grained forested landscapes is low compared to agricultural landscapes (e.g., Villard et al., 1999) and coarse-grained forested regions. In the latter landscapes, the contrast between suitable and unsuitable habitat for forest-associated species is distinct and may be more accurately represented by patches; habitat islands may more closely approximate oceanic islands and species-area relationships may be more pronounced (Brotons et al., 2003b).

4.3. Local and microhabitat associations

At a local scale, flying squirrels in our study area were more likely to occur at sites with old, mixedwood forest conditions. Snags and coarse woody debris were not important predictors of flying squirrel occurrence. This may be due to, in part, the current prevalence of these features following a spruce-bud worm outbreak in the 1970s. A similar lack of relationship between flying squirrel density and snag abundance was reported for an area with a high abundance of mistletoe (and therefore brooms for weatherproof nest sites; Lehmkuhl et al., 2006). A mixedwood association has been reported elsewhere in this species' range (southern Appalachians: Payne et al., 1989; northern Alberta: Wheatley et al., 2005). This association may relate to a higher diversity of food and nesting resources, possibly leading to more stable population dynamics. Plant material formed 22% of fall flying squirrel diets in the eastern Washington Cascade Range and may have provided important supplements to the flying squirrels' nutrient-poor truffle diet (Lehmkuhl et al., 2006). Deciduous tree volume in conifer-dominated stands and the percentage of potential habitat in the surrounding area were good predictors of patch occupancy by Siberian flying squirrels (Hurme et al., 2008). Interestingly, the coarse resolution of the provincial forest inventory precluded our detection of a mixedwood-association. A similar mixedwood forest association detectable only at a fine resolution was reported for Blackburnian warblers (*Dendroica fusca*) within our study area (Young et al., 2005).

4.4. Potential detection probability bias

It is possible that the effective sampling area varies according to site conditions (i.e., is habitat-mediated). We assessed whether capture success was biased by habitat conditions by using occupancy modeling (MacKenzie et al., 2002). We found no detection biases at local or neighbourhood scales; therefore it is unlikely that there was an effect of forest age on capture probability. We found some evidence that flying squirrels were more likely to be trapped at sites with greater amounts of open area in the surrounding landscape, making our estimates of their response to non-habitat matrix conservative. Possible reasons for this detection bias could include: (1) our traplines in these locations may have been established within high-use areas where individuals spend a disproportionate amount and therefore are more likely to encounter traps; (2) animals could be experiencing a 'fence effect' that discourages movement away from the vicinity when they encounter a boundary with non-habitat matrix (Bayne and Hobson, 1998); (3) traplines may have been situated in areas being used as travel corridors and therefore more likely to be encountered by individuals.

4.5. Management implications

The relative importance of landscape composition compared to configuration suggests that maintaining connectivity, while valuable for some species, cannot compensate for the negative impacts of decreased habitat amount for flying squirrels within our study area. Additionally, flying squirrels' negative association with

open, non-habitat matrix suggests the species may be particularly sensitive to forest management practices that leave treeless areas. A long-term study on effect of fragmentation and habitat loss in the Amazonian rainforest on birds, small mammals and frogs suggests that species that avoid the matrix (e.g., over-grown abandoned pastures) are more likely to disappear from remaining fragments (Gascon et al., 1999). The negative response of flying squirrels to non-habitat matrix could relate to a variety of factors, including reduced-movement efficiency, increased predation risk, competition and/or reduced food availability (Hamer et al., 2003; Lehmkuhl et al., 2006; Scheibe et al., 2006). Management practices that maintain high levels of canopy closure and preserve as much environmental heterogeneity (e.g., variable structure, stem density, species composition) as possible may reduce the effect of logging on flying squirrel movement behaviour and retain microhabitat conditions favorable for truffle and vascular plant food production (Lehmkuhl et al., 2006).

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References

- Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71, 355–366.
- Bakker, V.J., 2006. Microhabitat features influence the movements of red squirrels (*Tamiasciurus hudsonicus*) on unfamiliar ground. *Journal of Mammalogy* 87, 124–130.
- Bakker, V.J., Van Vuren, D.H., 2004. Gap-crossing decisions by the red squirrel, a forest-dependent small mammal. *Conservation Biology* 689–697.
- Banks, S.C., Lindenmayer, D.B., Ward, S.J., Taylor, A.C., 2005. The effects of habitat fragmentation on the social kin structure and mating system of the agile antechinus *Antechinus agilis*. *Molecular Ecology* 14, 1789–1801.
- Bascompte, J., Solé, R.V., 1996. Habitat fragmentation and extinction thresholds in spatially explicit models. *Journal of Animal Ecology* 65, 465–473.
- Bayne, E., Hobson, K., 1998. The effects of habitat fragmentation by forestry and agriculture on the abundance of small mammals in the southern boreal mixed-wood forest. *Canadian Journal of Zoology* 76, 62–69.
- Bélisle, M., 2005. Measuring landscape connectivity: the challenge of behavioural landscape ecology. *Ecology* 86, 1988–1995.
- Bélisle, M., Desrochers, A., 2002. Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. *Landscape Ecology* 17, 219–231.
- Bélisle, M., Desrochers, A., Fortin, M.J., 2001. Influence of forest cover on the movements of forest birds: a homing experiment. *Ecology* 82, 1893–1904.
- Bender, D.J., Fahrig, L., 2005. Matrix structure obscures the relationship between interpatch movement and patch size and isolation. *Ecology* 86, 1023–1033.
- Bender, D.J., Contreras, T.A., Fahrig, L., 1998. Habitat loss and population decline: a meta analysis of the patch size effect. *Ecology* 79, 517–533.
- Bender, D.J., Tischendorf, L., Fahrig, L., 2003. Using patch isolation metrics to predict animal movement in binary landscapes. *Landscape Ecology* 18, 17–39.
- Berggren, A., Carlson, A., Kindvall, O., 2001. The effect of landscape composition on colonization success, growth rate and dispersal in introduced bush-crickets *Metroptera roeselii*. *Journal of Animal Ecology* 70, 663–670.
- Betts, M.G., Franklin, S.E., Taylor, R.G., 2003. Interpretation of landscape pattern and habitat change for local indicator species using satellite imagery and geographic information system data in New Brunswick, Canada. *Canadian Journal of Forest Research* 33, 1821–1831.
- Betts, M.G., Forbes, G.J., Diamond, A.W., Taylor, P.D., 2006. Independent effects of habitat amount and fragmentation on songbirds in a forest mosaic: an organism-based approach. *Ecological Applications* 16, 1076–1089.
- Betts, M.G., Forbes, G.J., Diamond, A.W., 2007. Thresholds in songbird occurrence in relation to landscape structure. *Conservation Biology* 21, 1046–1058.
- Betts, M.G., Villard, M.-A., 2009. Landscape thresholds in species occurrence as quantitative targets in forest management: generality in space and time? In: Villard, M.-A., Jonsson, B.G. (Eds.), *Setting Conservation Targets for Managed Forest Landscapes*. Cambridge University Press, pp. 185–206.
- Bourgeois, M.C. 1997. An examination of two unconventional methods to assess resource use by two New Brunswick forest mammals: the marten and the northern flying squirrel. MSc. Thesis. Department of Biology, Acadia University, Wolfville, N.S. p. 68.
- Bowman, J., Fahrig, L., 2002. Gap crossing by chipmunks: an experimental test of landscape connectivity. *Canadian Journal of Zoology* 80, 1556–1561.
- Bowman, J., Jaeger, J.A.G., Fahrig, L., 2002. Dispersal distance of mammals is proportional to home range size. *Ecology* 83, 2049–2055.
- Brotos, L., Mönkkönen, M., Huhta, E., Nikula, A., Rajasarkka, A., 2003a. Effects of landscape structure and forest reserve location on old-growth forest bird species in Northern Finland. *Landscape Ecology* 18, 377–393.
- Brotos, L., Mönkkönen, M., Martin, J.L., 2003b. Are fragments islands? Landscape context and density-area relationships in boreal forest birds. *American Naturalist* 162, 343–357.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York, p. 488.
- Carey, A.B., 2000. Effects of new forest management strategies on squirrel populations. *Ecological Applications* 10, 248–257.
- Castellón, T.D., Sieving, K.E., 2006. An experimental test of matrix permeability and corridor use by an endemic understory bird. *Conservation Biology* 20, 135–145.
- Chevan, A., Sutherland, M., 1991. Hierarchical partitioning. *American Statistician* 45, 90–96.
- Cooper, C.B., Walters, J.R., 2002. Experimental evidence of disrupted dispersal causing decline of an Australian passerine in fragmented habitat. *Conservation Biology* 16, 471–478.
- D'Eon, R., Glenn, S.M., Parfitt, I., Fortin, M.J. 2002. Landscape connectivity as a function of scale and organism vagility in a real forested landscape [online]. *Conservation Ecology* 6, article 10 URL: <http://www.consecol.org/vol6/iss2/art10>.
- Desrochers, A., Hanski, I.K., Selonen, V., 2003. Siberian flying squirrel responses to high- and low-contrast forest edges. *Landscape Ecology* 18, 543–552.
- Drapeau, P., Leduc, A., Giroux, J.F., Savard, J.P.L., Bergeron, Y., Vickery, W.L., 2000. Landscape-scale disturbances and changes in bird communities of boreal mixed-wood forests. *Ecological Monograph* 70, 423–444.
- Dunning, J.B., Danielson, B.J., Pulliam, H.R., 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65, 169–175.
- Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M.C., Peterson, A.T., Phillips, S.J., Richardson, K.S., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151.
- Estrada, A., Coates-Estrada, R., Meritt, D., 1994. Non-flying mammals and landscape changes in the tropical rain-forest region of Los-Tuxtlas, Mexico. *Ecography* 17, 229–241.
- Fagan, W.E., Cantrell, R.S., Cosner, C., 1999. How habitat edges change species interactions. *American Naturalist* 153, 165–182.
- Fahrig, L., 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* 61, 603–610.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics* 34, 487–515.
- Fahrig, L., 2007. Non-optimal animal movement in human-altered landscapes. *Functional Ecology* 21, 1003–1015.
- Ficetola, G.F., de Bernardi, F., 2004. Amphibians in a human-dominated landscape: the community structure is related to habitat features and isolation. *Biological Conservation* 119, 219–230.
- Fischer, J., Lindenmayer, D.B., 2006. Beyond fragmentation: the continuum model for fauna research and conservation in human-modified landscapes. *Oikos* 112, 473–480.
- Fletcher, R., 2006. Emergent properties of conspecific attraction in fragmented landscapes. *American Naturalist* 168, 207–219.
- Fletcher Jr., R.J., Hutto, R.L., 2008. Partitioning the multi-scale effects of human activity on the occurrence of riparian forest bird. *Landscape Ecology* 23, 727–739.
- Gascon, C., Lovejoy, T.E., Bierregaard Jr., R.O., Malcolm, J.R., Stouffer, P.C., Vasconcelos, H.L., Laurance, W.F., Zimmerman, B., Tocher, M., Borges, S., 1999. Matrix habitat and species richness in tropical remnants. *Biological Conservation* 91, 223–229.
- Gerrow, J.S. 1996. Home range, habitat use, nesting ecology and diet of the northern flying squirrel in southern New Brunswick. M.Sc. Thesis. Department of Biology, Acadia University, Wolfville, N.S. p. 53.
- Guénette, J.-S., Villard, M.A., 2005. Thresholds in forest bird response to habitat alteration as quantitative targets for conservation. *Conservation Biology* 19, 1168–1180.
- Guerry, A.D., Hunter, M.L., 2002. Amphibian distributions in a landscape of forests and agriculture: an examination of landscape composition and configuration. *Conservation Biology* 16, 745–754.
- Hamer, K.C., Hill, J.K., Benedick, S., Mustafa, N., Sherratt, T.N., Maryati, M., Chey, V.K., 2003. Ecology of butterflies in natural and selectively logged forests of northern Borneo: the importance of habitat heterogeneity. *Journal of Applied Ecology* 40, 150–162.
- Hanski, I., 1998. Metapopulation dynamics. *Nature* 396, 41–49.
- Heikkinen, R.K., Luoto, M., Virkkala, R., Rainio, K., 2004. Effects of habitat cover, landscape structure and spatial variables on the abundance of birds in an agricultural-forest mosaic. *Journal of Applied Ecology* 41, 824–835.

- Hurme, E., Mönkkönen, M., Nikula, A., Nivala, V., Reunanen, P., Heikkinen, T., Ukkola, M., 2005. Building and evaluating predictive occupancy models for the Siberian flying squirrel using forest planning data. *Forest Ecology and Management* 216, 241–256.
- Hurme, E., Mönkkönen, M., Reunanen, P., Nikula, A., Nivala, V., 2008. Temporal patch occupancy dynamics of the Siberian flying squirrel in a boreal forest landscape. *Ecography* 31, 469–476.
- Hosmer, D.W., Lemeshow, S., 2000. *Applied Logistic Regression*. John Wiley & Sons, New York, p. 375.
- Jansson, G., Angelstam, P., 1999. Threshold levels of habitat composition for the presence of the long-tailed tit (*Aegithalos caudatus*) in a boreal landscape. *Landscape Ecology* 14, 283–290.
- Kurki, S., Nikula, A., Helle, P., Linden, H., 1998. Abundances of red fox and pine marten in relation to the composition of boreal forest landscapes. *Journal of Animal Ecology* 67, 874–886.
- Legendre, P., 1993. Spatial autocorrelations: trouble or new paradigm? *Ecology* 74, 1659–1673.
- Lehmkuhl, J.F., Kistler, K.D., Begley, J.S., Boulanger, J., 2006. Demography of northern flying squirrels informs ecosystem management of western interior forests. *Ecological Applications* 16, 584–600.
- Lichstein, J.W., Simons, T.R., Shriver, S.A., Franzreb, K.E., 2002. Spatial autocorrelation and autoregressive models in ecology. *Ecological Monograph* 72, 445–463.
- Lidicker Jr., W.Z., 1999. Responses of mammals to habitat edges: an overview. *Landscape Ecology* 14, 333–343.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83, 2248–2255.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E., 2005. *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Academic Press, Burlington, p. 344.
- Manel, S., Williams, H.C., Ormerod, S.J., 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology* 38, 921–931.
- McGarigal, K., McComb, W.C., 1995. Relationships between landscape structure and breeding birds in the Oregon coast range. *Ecological Monograph* 65, 235–260.
- McGarigal, K., Cushman, S.A., Neel, M.C., Ene, E., 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. University of Massachusetts, Amherst. Available from www.umass.edu/landeco/research/fragstats/fragstats.html [accessed 13 August 2008].
- Moilanen, A., Nieminen, M., 2002. Simple connectivity measures in spatial ecology. *Ecology* 83, 1131–1145.
- Mönkkönen, M., Reunanen, P., 1999. On critical thresholds in landscape connectivity: a management perspective. *Oikos* 84, 302–305.
- Mönkkönen, M., Reunanen, P., Nikula, A., Inkeroinen, J., Forsman, J., 1997. Landscape characteristics associated with the occurrence of the flying squirrel *Pteromys volans* in old-growth forests of northern Finland. *Ecography* 20, 634–642.
- Payne, J.L., Young, D.R., Pagels, J.F., 1989. Plant community characteristics associated with the endangered northern flying squirrel *Glaucomys sabrinus* in the southern Appalachians USA. *American Midland Naturalist* 121, 285–292.
- Pimm, S.L., Russell, G.J., Gittleman, J.L., Brooks, T.M., 1995. The future of biodiversity. *Science* 269, 347–350.
- Pulliam, H.R., Danielson, B.J., 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist* 137, S50–S66.
- R Development Core Team, 2005. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. Available from www.r-project.org [accessed 13 August 2008].
- Radford, J.Q., Bennett, A.F., 2007. The relative importance of landscape properties for woodland birds in agricultural environments. *Journal of Applied Ecology* 44, 737–747.
- Radford, J.Q., Bennett, A.F., Cheers, C.J., 2005. Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biological Conservation* 124, 317–337.
- Reunanen, P., Mönkkönen, M., Nikula, A., Hurme, E., Nivala, V., 2004. Assessing landscape thresholds for the Siberian flying squirrel. *Ecological Bulletin* 21, 277–286.
- Rodewald, A.D., Yahner, R.H., 2001. Influence of landscape composition on avian community structure and associated mechanisms. *Ecology* 82, 3493–3504.
- SAS Institute Inc., 2002. Version 9.1. SAS Institute Inc., Cary, NC, USA.
- Scheibe, J.S., Smith, W.P., Bassham, J., Magness, D., 2006. Locomotor performance and cost of transport in the northern flying squirrel *Glaucomys sabrinus*. *Acta Theriologica* 51, 169–178.
- Selonen, V., Hanski, I.K., 2003. Movements of the flying squirrel *Pteromys volans* in corridors and in matrix habitat. *Ecography* 26, 641–651.
- Selonen, V., Hanski, I.K., 2004. Young flying squirrels (*Pteromys volans*) dispersing in fragmented forests. *Behavioral Ecology* 15, 564–571.
- Shaffer, T.L., 2004. Logistic-exposure analyses of nest survival. Jamestown, Northern Prairie Wildlife Research Center Online. Available from www.npwr.usgs.gov/resource/birds/nestsurv/index.htm [accessed 13 August 2008].
- Schipper, et al., 2008. The status of the World's land and marine mammals: diversity, threat, and knowledge. *Science* 322, 225–230.
- Smith, W.P., 2007. Ecology of *Glaucomys sabrinus*: habitat, demography, and community relations. *Journal of Mammalogy* 88, 862–881.
- Smith, W.P., Person, D.K., 2007. Estimated persistence of northern flying squirrel populations in temperate rain forest fragments of Southeast Alaska. *Biological Conservation* 137, 626–636.
- Timber Management Branch. New Brunswick forest inventory (1986) report. NRE/RNE 89-01-003. Natural Resources and Energy, Fredericton, N.B. p. 302.
- Tischendorf, L., Bender, D.J., Fahrig, L., 2003. Evaluation of patch isolation metrics in mosaic landscapes for specialist vs generalist dispersers. *Landscape Ecology* 18, 41–50.
- Trzcinski, M.K., Fahrig, L., Merriam, G., 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecological Applications* 9, 586–593.
- Turner, M.G., 1989. Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* 20, 171–197.
- Umetsu, F., Metzger, J.P., Pardini, R., 2008. Importance of estimating matrix quality for modeling species distribution in complex tropical landscapes: a test with Atlantic forest small mammals. *Ecography* 31, 359–370.
- Underwood, A.J., 2001. *Experiments in Ecology: Their Logical Design and Interpretation using Analysis of Variance*. Cambridge University Press, Cambridge, p. 522.
- Van Buskirk, J., 2005. Local and landscape influence on amphibian occurrence and abundance. *Ecology* 86, 1936–1947.
- Vernes, K., 2004. Breeding biology and seasonal capture success of northern flying squirrels (*Glaucomys sabrinus*) and red squirrels (*Tamiasciurus hudsonicus*) in southern New Brunswick. *Northeastern Naturalist* 11, 123–136.
- Vida, S., 2001. *AccuRoc for Windows*. Accumetric Corp., Montreal.
- Villard, M.A., Trzcinski, M.K., Merriam, G., 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conservation Biology* 13, 774–783.
- Weigl, P.D., 2007. The northern flying squirrel (*Glaucomys sabrinus*): a conservation challenge. *Journal of Mammalogy* 88, 897–907.
- Wheatley, M., Fisher, J.T., Larsen, K., Litke, J., Boutin, S., 2005. Using GIS to relate small mammal abundance and landscape structure at multiple spatial extents: the northern flying squirrel in Alberta, Canada. *Journal of Applied Ecology* 42, 577–586.
- Wiegand, T., Revilla, E., Moloney, K.A., 2005. Effects of habitat loss and fragmentation on population dynamics. *Conservation Biology* 19, 108–121.
- Wiens, J.A., 1989. Spatial scaling in ecology. *Functional Ecology* 3, 385–397.
- With, K.A., Crist, T.O., 1995. Critical thresholds in species' responses to landscape structure. *Ecology* 78, 2446–2459.
- Young, L., Betts, M.G., Diamond, A.W., 2005. Do Blackburnian Warblers select mixed forest? The importance of spatial resolution in defining habitat. *Forest Ecology and Management* 214, 358–372.
- Zollner, P.A., 2000. Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. *Landscape Ecology* 15, 523–533.