Research article

The protean relationship between boreal forest landscape structure and red squirrel distribution at multiple spatial scales

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Abstract

This paper investigates two fundamental questions in landscape ecology: what influence does landscape context, or the composition of the matrix, have on an animals' response to landscape structure, and how does this relationship extrapolate between landscapes? We investigate how the distribution of North American red squirrels (*Tamiasciurus hudsonicus*) in the boreal mixedwood forest is influenced by anthropogenically (forest harvest) and naturally (forest fire) derived landscape structure. We studied the presence and absence of red squirrels over two years in three landscape types: one managed for timber harvest, one recently burned by wildfire, and a third unburned unmanaged landscape. Landscape composition and configuration, measured at several spatial scales, predicted red squirrel's distribution in all three landscapes, but the significant landscape variables changed across spatial scales, across time, and across landscapes. These findings emphasize the variability in landscape structure/animal distribution relationships, and enforce the need to link pattern-finding studies, such as this one, with searches for the mechanisms behind the observed pattern.

Introduction

The influence of landscape structure – used here to collectively describe composition and configuration – on animal distribution has often been tested in anthropogenically modified landscapes. Anthropogenic landscapes, such as agricultural areas, often exhibit high levels of fragmentation, wherein natural habitat is left as small disjunct patches within a matrix of unsuitable habitat (e.g., Wegner and Merriam 1979; Middleton and Merriam 1983; Henein et al. 1998). The quality or composition of the matrix has been implicated as a driver of observed distribution patterns within suitable patches in such anthropogenically fragmented systems (Fisher and Merriam 2000; Steffan-Dewenter 2003). Natural environments are also patchy (Wiens 1976); and although less studied, the

matrix in naturally heterogeneous landscapes may influence patch use (see Turner et al. 2001 for review; Brotons et al. 2003; but see Edenius and Sjöberg 1997). The relationship between landscape structure and animal distribution could markedly differ between landscape contexts – for example, between natural and anthropogenic forest landscapes – due to the relatively soft edges and low contrast in natural landscapes compared with anthropogenic ones (Mönkkönen and Reunanen 1999).

Several mechanisms driving species' response to landscape structure have been identified. Response to landscape structure has been found to be species-specific (see Wegner and Merriam 1979; Middleton and Merriam 1983). This specificity is often attributed to behavioural differences, degree of habitat specialisation, and levels of adaptive flexibility (Bright 1993;

Andrén 1994; Andrén et al. 1997; Henein et al. 1998). For example, a species' response to landscape structure depends on its perception of grain and extent (Kotliar and Wiens 1990). Larger vagile organisms perceive a finer-grain mosaic than smaller, less vagile organisms. Hence, an organism's grain of perception can affect its response to landscape heterogeneity, and can define the extent of the functional landscape (Kotliar and Wiens 1990; Corkum 1999; Johnson et al. 2001). In addition to grain of perception, response to heterogeneity is also influenced by the spatial and temporal scale of significant ecological processes (such as dispersal or foraging) acting on, or exhibited by, an organism (Addicott et al. 1987). Thus, habitat specificity, habitat availability, and spatial context, can all influence what might be considered a 'functional landscape', and by extension, will influence the relationship between landscape structure and a species' distribution.

The fundamental assumption behind the search for relationships between landscape structure and animal distribution, and the associated mechanisms, is that these effects are consistent; that broad generalisations can be made and used to extrapolate across different landscapes. Merriam's work on landscape connectivity (Merriam 1988, 1991; see also Baudry and Merriam 1988; Taylor et al. 1993) is one area where consistency across landscapes has been demonstrated. Connectivity aside, research has rarely been undertaken to test the assumption that the response to landscape structure from one area can be extrapolated to another. Studies that have addressed this issue suggest that a species' response to landscape structure has a limited scope of inference (Rodríguez and Andrén 1999; Reunanen et al. 2002). The search for a common mechanism is futile if the assumption of consistency is violated, an issue hotly debated in discussions of generality and inference in ecology (e.g., Beck 1997; Lawton 1999). Obtaining an understanding of an organism's response to natural and anthropogenic heterogeneity is key to interpreting the mechanisms responsible for a response to landscape structure.

This study was designed to determine whether landscape structure in naturally heterogeneous areas could predict animal distribution, and to assess the generality of this relationship by comparing across three boreal landscapes. We measured the presence or absence of a conifer specialist, *Tamiasciurus hudsonicus,* within these heterogeneous areas. *T. hudsonicus*, the North American red squirrel, feeds primarily on the seeds found in the cones of conifer trees such as *Picea* and *Pinus* spp. (Smith 1968; Kemp and Keith 1970; Rusch and Reeder 1978; Riege 1991). Although red squirrels also feed on mushrooms, berries, and nuts (Gurnell 1983; Yahner 1987), they rely entirely on conifer cones for overwinter survival (Rusch and Reeder 1978). Hence, from a food supply perspective conifer stands are suitable habitat, whereas deciduous stands are poor habitat. We therefore postulated that red squirrels would perceive mixedwood boreal landscapes comprised of conifer, deciduous, and other stand types as heterogeneous, and that such a landscape is a mosaic of suitable patches embedded in a less suitable matrix.

We asked three questions, relating to relationships between landscape structure and animal distribution, spatial scale, and the scope of inference of these relationships:

1. Is there a relationship between landscape structure derived from natural heterogeneity, and red squirrel presence?
2. If so, is the relationship between landscape structure and squirrel presence similar as the spatial extent of a landscape varies?
3. Is the relationship between landscape structure and squirrel presence similar across three landscapes with different compositions and different sources of heterogeneity?

Methods

Study area

This study was conducted in the northern region of the Province of Alberta, Canada (Figure 1). This area lays within the mixedwood boreal forest and is covered mainly by black spruce (*Picea mariana*) bogs in hygric areas; aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) mixed sparsely with white spruce (*Picea glauca*) in mesic areas; and jack pine (*Pinus banksiana*) in xeric areas (Strong and Leggat 1992). Harvesting of aspen and conifer in some areas began in the early 1990's. All cutblocks in the study area were less than 10 years old.

Sampling design

Three areas were selected as part of the Sustainable Forest Management Network of Centres of

Figure 1. Mercator projection of North America, with the Province of Alberta, Canada, shaded. The location of the study areas within Alberta, in relation to major cities and water bodies, are marked with a star.

Excellence (SFM-NCE) Landscape Structure and Biodiversity Project, of which this study was a part. The Reference Area was unmanaged and unburned, 63 km^2 in size, with a central coordinate of 55° W 112°30′ N, near Lac La Biche, Alberta (Figure 1). Heterogeneity in the Reference Area was typical of natural boreal systems, resulting from old natural disturbances that have since regenerated, and microtopographical influences. The Managed Area was 63 km^2 in size, centred on 55°5′ W 112°15′ N, near Lac La Biche, Alberta (Figure 1). The Managed Area was similar in composition to the Reference Area, but had ca. 9% of its area commercially harvested within the last ten years. This was first-rotation harvest and occurred in a dispersed pattern. The Burned Area was smaller, *ca.* 40 km^2 in size, and centred on 55°30′ W 112°0′ N, near Goodwin Lake, Alberta (Figure 1). The Burned Area contained patches of unburned residual stands embedded within a burned matrix from a 1994 (3 year-old) fire. In all Areas, pre-disturbance landscapes were primarily composed of a matrix of deciduous trees with patches of conifer embedded within them.

Within the Managed and Reference Areas, a systematic sampling grid was installed, with points 1 km apart in a seven by nine pattern. This systematic system was chosen to accommodate the objectives of several studies conducted concurrently on these areas, involving forest songbirds, small mammals, insects, and amphibians. It was designed to pre-empt *a priori* assumptions associated with stratified designs, and to facilitate a variety of spatial analyses. To reduce confounds introduced by point-specific habitat differences, only upland sites were sampled. Points falling within a black spruce bog or other wetlands were dropped, and others added to the edges of the grid to compensate. In the Managed Area in 1996, 64 points were sampled for red squirrel presence. In 1997

Table 1. Reclassification protocol applied to Alberta Vegetation Index forest inventory maps to produce the landscape composition variables used in analyses. These variables plus burn-classified variables, where appropriate, were included in regression analyses.

Variable	Description	AVI Forest Cover Type	Relative Amount
CUT	cutblock	harvested	
DEC	deciduous	trembling aspen balsam poplar, birch	pure or mixed
MARSH	wet areas	non-forest type	
MDP	mixed deciduous/pine	DEC and jack pine/lodgepole pine	70–80%/20–30%
MDS	mixed deciduous/spruce	DEC and white spruce, black spruce, larch, or balsam fir	70–80%/20–30%
PJ	pine or pine mix	jack pine/lodgepole pine	Pure
		or	
		jack pine/lodgepole pine	70–80%
		and	
		larch, black spruce, white spruce, or balsam fir	20–30%
SBLT	black spruce/larch bog	black spruce or larch	Pure
		or	
		black spruce/larch	70–80%
		and	
		jack pine, lodgepole pine, white spruce, or balsam fir	20–30%
SW	white spruce	white spruce/balsam fir	Pure
		or	
		white spruce/balsam fir	70–80%
		and	
		larch, black spruce, lodgepole pine, or jack pine	20–30%

only 58 points were sampled, due to logistical issues. In the Reference Area, 63 points were sampled. Severely limited ground access precluded implementation of a systematic design in the Burned Area, so a stratified design was employed. We placed points at least 1 km apart, with points in each upland patch type; 29 sampling points were established in this Area. The Reference and Burned Areas were sampled only in 1997.

To quantify landscape structure, we used digital Alberta Forest Inventory data that described canopy closure, dominant and subordinate stand types, and year of origin. Polygons in these coverages were reclassified using Arc/Info GIS (Esri, Inc.) to describe the landscape based on dominant stand types. This level of resolution was based on previous studies of red squirrel habitat patch use and ecology (e.g., Smith 1968; Kemp and Keith 1970; Rusch and Reeder 1978). This reclassification yielded ten forest cover classes on the Managed and Reference Areas (Table 1). On the Burned Area, the dominant tree species within the polygon was combined with burn information to further categorize the polygon as burned lowland (burned SBLT or MARSH, designated BU-LOW), burned deciduous (BDEC), or burned pine (BPINE) (Table 2).

The landscape structure around each grid point was quantified using FRAGSTATS (McGarigal and Marks 1994) at five spatial scales. Landscape boundaries of

Table 2. Relative percentage of each habitat type (landscape composition variable) on the Reference, Managed, and Burned Areas.

Variable	Reference area	Managed area	Burned area
CUT (<10 years)	2%	9%	2%*
DEC	40%	43%	12%
MDP	3%	2%	<1%
MDS	1%	1%	N/A
PJ	18%	7%	2%
SBLT	22%	21%	10%
SW	2%	2%	N/A
BDEC	N/A	N/A	2%
BSBLT	N/A	N/A	34%
BPJ	N/A	N/A	7%
Other**	12%	15%	31%

*Burned, then salvaged logged; **Includes marsh, agriculture, roads, oil wells, and other non-forested sites.

50-m, 100-m, 250-m, 500-m, and 1000-m radii were created around each grid point. These scales were assumed to encompass a range of ecological neighbourhoods (*sensu* Addicott 1987) for red squirrels, including small scales corresponding to squirrels' summer foraging range (50 m to 100 m; Fisher 1999) and larger scales (100–1000 m) relating to dispersal (Larsen and Boutin 1994). Variables describing landscape composition (Table 1, Table 2) and landscape configuration (including edge density, largest patch index, mean patch size, mean shape index, patch density, patch richness density, and Simpson's

evenness index) at each scale, around each point, were calculated for the reclassified forest inventory coverages. Landscape composition variables had a Poisson distribution, so were transformed using the arcsin {square root (p)} transformation (Zar 1996) to approximate a normal distribution.

Some landscape composition variables were collinear (Pearson correlations, $p < 0.05$, SPSS Inc.). For instance, in the Managed Area at the 500-m scale where landscapes tended to be binary, DEC and SBLT were negatively correlated. However, this collinearity was not consistent between Areas or between scales. In the Reference Area DEC, SBLT, and PJ were prevalent, thus reducing collinearity between any two (see Corkum et al. 1999 for further analysis and discussion of multicollinearity in these variables). Our aim was to perform consistent, standard analyses across scales and Areas, so landscape composition variables were not removed or reduced. However, landscape configuration variables generated by FRAGSTATS were consistently collinear with dominant composition variables in each Area, and with each other in all Areas (Pearson correlations, $p < 0.05$; Corkum et al. 1999). To overcome this problem, we condensed the many landscape configuration variables into a single measure. We entered edge density, largest patch index, mean patch size, mean shape index, patch density, patch richness density, and Simpson's evenness index – variables representing landscape heterogeneity and patchiness – into a principal components analysis (PCA; SPSS Inc. 1996). A PCA was run for landscape configuration variables generated at each scale, within each grid, within each area. This analysis incorporated information from each configuration variable into a single component that consistently explained most of the variation within each scale, grid, and area for which it was created (Fisher 1999; Corkum et al. 1999). We termed this component heterogeneity (HET). Essentially, as HET increased, so did edge density, mean shape index, patch density, patch richness, and evenness; largest patch index and mean patch size decreased. This HET variable was used to represent landscape configuration in further analyses.

Squirrel surveys

Presence/absence data for red squirrels were obtained through call surveys. Points were visited four times over the summers of 1996 (Managed Area only) and 1997 (all Areas). The occurrence of red squirrel territorial calls over a ten-minute period were noted at each visit. Thus, for each point 40 minutes were sampled, well exceeding territorial call rates for red squirrels (S. Boutin, unpubl. data). Only audible calls originating from squirrels within 50 m of the sample point were included in our analyses. Thus, within a given year, we could confidently designate squirrels 'present' at a sampling station where at least one call was heard, and 'absent' where they were not, yielding a binary response variable.

Statistical analysis

To examine differences in the explanatory power of landscape structure at different scales, logistic regression analyses (SPSS Inc. 1996) were used to search for relationships between squirrel presence/absence and the landscape variables on the Managed, Burned, and Reference Areas. We ran separate regressions of squirrel presence/absence against landscape variables computed at each of the 50, 100, 250, 500, and 1000-m scales. That is, composition variables (Table 1, Table 2), HET, and interaction terms between HET and composition variables – measured at a single spatial scale – were entered into each model. For the 1000 m-scale analysis on the Managed and Reference Areas, adjacent points were dropped systematically to prevent overlap and maintain independence between circular landscapes. Points in the Burned Area were not distant enough from one another to allow a 1000-m scale analysis.

Multiple logistic regressions employed a forward conditional selection procedure with a significance for inclusion criterion of $p = 0.05$ (SPSS Inc. 1996) as this method reveals those predictor variables that explain the most variation in the response variable (Hosmer and Lemeshow 1989; Menard 1995). Nagelkerke R^2 (Nagelkerke 1991) was used to compare each of the logistic regression models. This is a measure of deviance explained, analogous to variance explained in linear regression models, in that it describes the strength of the relationship between dependent and independent variables. As differences in squirrel saturation of the landscape may confound our ability to detect actual changes in response to landscape structure between years, a sign test (Zar 1996) was used to test for significant differences in squirrel presence/absence between 1996 and 1997 on the Managed Area grid.

Results

Squirrel presence

Red squirrels were detected at 38 of 64 points (59%) on the Managed Area grid in 1996, and at 26 of 58 points (49%) in 1997. A sign test (Zar 1996) indicated no significant differences ($p > 0.05$) in squirrel presence/absence between 1996 and 1997 on the Managed Area grid. Squirrels were detected at 31 of 63 points (49%) in the Reference Area, and at 7 of 29 sites (24%) in the Burned Area.

Logistic regression models

On the Managed Area in 1996, the deviance explained by landscape structure peaked at 100 m but was roughly similar across all scales except 1000 m, where no variables predicted squirrel presence (Figure 2a). HET positively predicted squirrel presence at the 50 m scale; jack pine (PJ) was the only significant composition variable. There was a positive relationship with the heterogeneity/deciduous interaction term (HET*DEC), and a positive relationship with black spruce, at 100 m. There was a negative relationship with DEC, and a positive relationship with SBLT, at 250 m and 500 m. HET was not significant at 250 m or 500 m, as it was at smaller scales.

On the Managed Area in 1997, the relationships differed from those observed the previous year. In 1997 the R^2 of the models decreased from 50 m to 250 m, then increased from 250 m to 1000 m (Figure 2b). The model R^2 was highest at the 1000-m scale in 1997, whereas in 1996 the 1000-m model was not significant. HET was not significant at smaller scales, but was significant at larger scales – a trend opposite to that observed in 1996. Black spruce was significant at all scales except the 50-m scale. Jack pine (PJ) was significant at all scales in 1997, as opposed to only the 50-m scale in 1996. There was a negative relationship with the SBLT*HET interaction term at the 500-m scale, but a positive relationship with the PJ*HET interaction term at 1000 m.

The relationships seen on the Reference Area were different from those observed on the Managed Area (Figure 3). Predictive power was greatest at the 250-m scale. Deciduous cover was a significant negative predictor of squirrel presence at 50 m and 250 m. Conifer composition variables were significant at the 100-m and 250-m scales. There were no significant predictors at the 1000-m scale. Neither HET, nor any
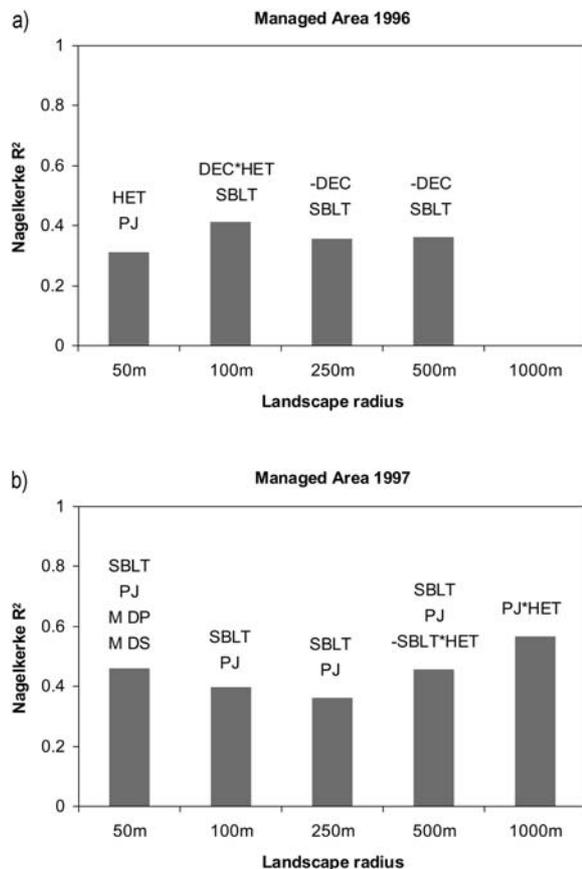

Figure 2. The deviance explained by multiple logistic regression models in which squirrel presence was regressed against landscape structural variables in the Managed Area in (a) 1996 (n = 64) and (b) 1997 (n = 58). The significant variables ($p < 0.05$) are listed on top of the deviance bars in the order in which they entered the model. Explanations of variable acronyms are listed in Table 1.

HET*composition interaction terms, were significant at any scale in the Reference Area, unlike the Managed Areas.

The statistical relationships between landscape structure and squirrel presence on the Burned Area were different from those in both the Managed and Reference Areas. In the Burned Area, landscape variables were significant only at the 50-m and 100-m scales; there were no significant models at 250-m and 500-m scales (Figure 4). Nagelkerke R^2 was highest at the 50-m scale. Unburned mixed deciduous/pine (MDP) cover was important at both scales. The negative HET*DEC interaction term was significant at the 50-m scale. Deciduous cover (DEC) was a positive predictor at 100 m, unlike all other Areas at all other scales.
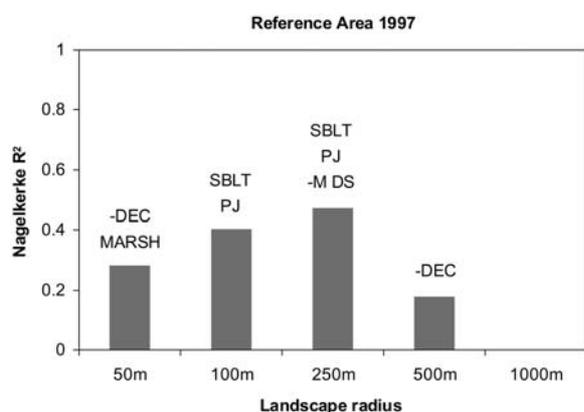
Reference Area 1997

Figure 3. The deviance explained by multiple logistic regression models in which squirrel presence was regressed against landscape structural variables in the Reference Area (n = 63). The significant variables (p < 0.05) are listed on top of the deviance bars in the order in which they entered the model. Explanations of variable acronyms are listed in Table 1.
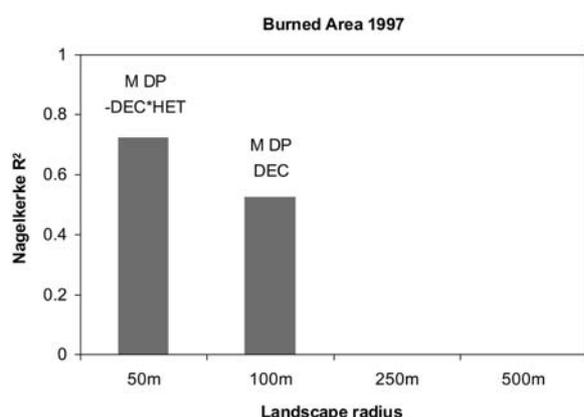
Burned Area 1997

Figure 4. The deviance explained by multiple logistic regression models in which squirrel presence was regressed against landscape structural variables in the Burned Area (n = 29). The significant variables (p < 0.05) are listed on top of the deviance bars in the order in which they entered the model. Explanations of variable acronyms are listed in Table 1.

Discussion

Landscape structure derived from natural heterogeneity did predict red squirrel distribution. Response to landscape structure is not an artefact of anthropogenic modification of habitat configuration and composition, but is instead an inherent function of inhabiting patchy environments. Although this should be intuitive, it prompts us to look beyond the patterns, to consider the mechanisms that are effecting these responses, and to determine why patterns might differ between different landscapes.

The relationship between landscape structure and squirrel presence was not constant as the spatial extent of a landscape varied. Not only did the amount of variation explained by the models change with scale, the variables that became significant predictors of squirrel presence changed as well. The models describing the relationship between landscape structure and red squirrel abundance changed between Areas or landscape contexts. These disparities concur with previous theoretical (Mönkkönen and Reunanen 1999) and empirical (Bowman et al. 2001; Brotons et al. 2003; Steffan-Dewenter 2003) work, and highlight the problem associated with assigning importance to habitat types, or landscape configurations, based on studies conducted at only one scale or in one landscape context. Our results suggest that the landscape structure/red squirrel distribution relationship is dependent on a number of complex factors.

Time-dependent responses

The relationship between squirrel presence and landscape structure changed between the summers of 1996 and 1997 on the Managed Area. Similarly, van Apeldoorn et al. (1994) found that the landscape variables that significantly predicted Eurasian red squirrel (*Sciurus vulgaris*) presence changed through time. They attributed these changes to variations in individual spatial behaviour during an overall increase in squirrel abundance in their study area. Our comparison of squirrel presence across years indicated that the dynamism in observed landscape relationships was not due to differences in red squirrel saturation of the landscape over time. Instead, the specific points occupied by squirrels changed; it follows that the mechanism driving the response to landscape structure may have changed between years. North American red squirrels are conifer specialists, generally preferring white spruce over jack pine, and jack pine over black spruce (Smith 1968; Kemp and Keith 1970; Rusch and Reeder 1978). Wheatley et al. (2002) studied red squirrel demography in these patch types during a white spruce cone failure, and found that changes in conifer cone production between years altered the relative quality of these three patch types. This change in quality was reflected in red squirrel density, reproductive rates, and stand occupancy. In addition, red squirrels are known to undertake a 'spring shuffle' wherein they abandon traditional territories in favour of obtaining newly available,

higher-quality territories (Rusch and Reeder 1978), sometimes in different patch types (Wheatley et al. 2002). Such a switch in patch type preference may be indicated in our study by the appearance of jack pine as a significant predictor on the Managed Area in 1997, whereas it was rarely significant in 1996. Unfortunately, we did not obtain data on conifer cone availability or other temporally variable measures of stand-level habitat quality, so this remains a hypothesis – as the food source is temporally dynamic, the relationship between landscape structure and squirrel distribution is likewise dynamic. Landscape ecology studies should be conducted over long time-frames, as the nature of the temporal dynamism in the landscape/ animal distribution relationship may yield important clues to the mechanism behind it.

Scale-dependent responses

Red squirrel presence was related to landscape structure at a number of different spatial extents. A scale-dependent response to landscape structure was also found for deer mice (*Peromyscus maniculatus*) and red-backed voles (*Clethrionomys gapperi*) within these study Areas (Corkum 1999). Our results may suggest that more than one ecological mechanism was responsible for the observed pattern in squirrel distribution. We hypothesise that squirrels' response to heterogeneity at small scales, individuals' use of several adjacent patch types, and the existence of larger foraging ranges in areas where conifer is limiting (Fisher 1999), suggest that landscape supplementation (Dunning et al. 1992) is occurring. That is, in a landscape where conifer stands are sparse and embedded in a matrix of deciduous habitat that provides alternative ephemeral food resources, squirrels use this matrix to supplement resources provided by the limited prime conifer habitat. Additionally, the response to landscape structure at larger scales may suggest that processes encompassing larger areas, such as red squirrel dispersal (Larsen and Boutin 1994), and the 'spring shuffle' (Rusch and Reeder 1978; Wheatley et al. 2002), may be involved. In the Managed Area, there existed at large scales a positive relationship with large homogeneous conifer tracts representing comparatively good habitat. We hypothesise that this relationship could be indicative of a source-sink dynamic (Pulliam 1988; Pulliam and Danielson 1991), as suggested by the higher probability of squirrel presence in patches proximal to large contiguous tracts of optimal habitat that are presum-

ably producing a surplus of individuals. In a pattern-seeking study such as this one, we cannot begin to ascribe mechanisms, but testing for the presence of these mechanisms, or their relative importance if several are working concurrently, should be the focus of future work.

Context-dependent responses

We found that the relationship between boreal forest landscape structure and red squirrel distribution differed between the Burned, Managed, and Reference areas. Bowman et al. (2001) also suggested that relationships between boreal forest landscape structure and small mammal abundance were landscape context-specific. Similarly, landscape models of Eurasian red squirrel abundance (Rodríguez and Andrén (1999) and Siberian flying squirrel distribution (Reunanen et al. 2002) derived from one landscape could rarely be accurately extrapolated to other landscapes. Red squirrel response to landscape structure was mediated by the spatial arrangement of habitat and variation in the quality of the matrix (Rodríguez and Andrén 1999). Differences in flying squirrel model efficacy were attributed to differences in connectivity between two different landscape matrices, wrought by differences in the extent of forest matrix regeneration following forest harvesting (Reunanen et al. 2002). Changes in response to landscape structure between contexts may suggest that different mechanisms drive squirrels' response to heterogeneity in different contexts. By corollary, the net effect of a particular patch type may differ between contexts. Hence in our Burned Area red squirrels were found mainly in intact deciduous patches – in a landscape context where conifer is burned, intact deciduous was the most suitable habitat. In the Managed and Reference Areas, deciduous patches were negative predictors of squirrel presence due to a paucity of conifer seed required for overwinter survival; conifer was prime habitat. Our findings suggest that to extrapolate specific relationships from one area to another, without a fundamental understanding of the mechanisms involved, would be erroneous.

Further replication, and implementation of a sampling regime that encompasses the full range of each landscape variable (Vaughan and Ormerod 2003) could strengthen our design. Multicollinearity of landscape variables was rare but unavoidable when duplicating analyses across landscapes, and can influence model results. However, *a priori* knowledge

of red squirrel habitat use allowed us to critically assess logistic models, and frame ecological hypotheses to explain them. This knowledge also allowed us to avoid problems associated with spatial autocorrelation (Sokal and Oden 1978; Legendre 1993) by spacing points adequately to preserve independence.

Our results suggest that the ecological importance of patch types may change between scales, years, and landscape contexts, and that the scope of inference of landscape structure / animal distribution relationships can be limited. Thus, as well as yielding answers to our three questions, this paper also poses another crucial question: under what circumstances are certain patch types, or landscape structures, important predictors of animal occupation? We can conclude that these effects are context-specific, but the nature of that specificity remains the salient ecological issue.

Although landscape ecology is firmly entrenched in conservation-oriented studies of anthropogenic systems (see for example Forman 1997), our results indicate that the influence of structure is also a naturally occurring phenomenon in heterogeneous areas. We also know that the nature of these effects are not easily extrapolated from one year, scale, habitat type, or area, to the next. The search for processes to explain these inconsistencies will require a marriage of landscape ecology and population ecology – a demographic study that explicitly considers landscape structure as a treatment effect. Such a course of study will take us one step closer to understanding the protean nature of ecological systems, and the role of landscape variability in shaping those patterns.

Acknowledgements

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