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Landscape context and small-mammal abundance in a managed forest

Jeff Bowman^{b,c,*}, Graham Forbes^a, Tim Dilworth^b

^aNew Brunswick Cooperative Fish and Wildlife Research Unit, P. O. Box 45111, University of New Brunswick,
Fredericton, NB, Canada E3B 6E1

^bDepartment of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario, Canada K1S 5B6

^cTexas Tech University, Department of Range, Wildlife, and Fisheries Management, College of Agricultural Sciences
and Natural Resources, Box 42125, Lubbock, TX, 79409-2125, USA

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Abstract

We assessed whether small-mammal abundance was related to landscape context, when context was considered independently of within-stand vegetation and at different spatial extents. The study took place in an industrial forest in northwestern New Brunswick. Within-stand vegetation models explained 9–32% of the deviance in the abundance of individuals from the four most abundant species: red-backed voles; deer mice; short-tailed shrews; and woodland jumping mice. Landscape context was related to the distributions of two species: red-backed voles were less abundant within contexts of softwood plantations; and jumping mouse abundance was directly related to the amount of softwood forest. Variables measured at the largest radii of landscape context (500 m) were never significantly associated with the abundance of small mammals. Most species appeared robust to forest management with the exception of the negative relationship between red-backed voles and softwood plantations. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

Forest management can influence populations of small mammals in at least two ways: (1) by altering conditions within forest stands; or (2) by altering conditions around stands (i.e., altering the landscape context). Although the effects on small-mammal populations of landscape context in managed forests are not well known, the within-stand effects of various forest management interventions have been studied and have generally indicated that small-mammal

populations are robust. For example, Kirkland (1990) reviews 21 published studies to demonstrate that in eastern North America, many small-mammal species respond positively to clear cutting. He suggests that this response is due to the increased amount of herbaceous understory foliage on recently cut sites. Similarly, a number of stand-scale studies demonstrate that small-mammal populations either respond positively, or do not respond to selection (or partial) cutting (Swan et al., 1984; Monthey and Soutiere, 1985; Medin and Booth, 1989; Steventon et al., 1998). Broadly, it seems that there is a positive relationship between small-mammal populations and the amount of understory foliage. Thus, stand interventions that

* Corresponding author.

E-mail address: jbowman@ttacs.ttu.edu (J. Bowman).

reduce the amount of herbaceous understory (e.g., herbicide application, mechanical site preparation, softwood plantations) also reduce populations of folivorous small mammals until such a time as the understory regrows (Langley and Shure, 1980; Parker, 1989; Lautenschlager, 1993).

The removal of coarse woody debris (CWD) associated with some stand interventions (e.g., scarification) can be deleterious to small-mammal populations (see Harmon et al., 1986; Freedman et al., 1996 for reviews). Dead logs are a source of fungi and mycophagous small mammals (e.g., *Clethrionomys*) use CWD for foraging (Maser and Trappe, 1984). The distribution of mycophagous small mammals has been linked to the distribution of CWD (Nurdyke and Buskirk, 1991; Bowman et al., 2000a).

The many studies of within-stand effects of forest management on small mammals demonstrate a wide range of often species-specific relationships. However, few studies assess these relationships at the scale of a forest landscape. By forest landscape, we refer to spatial extents larger than single forest stands. The studies that do exist suggest, like many within-stand studies, that small-mammal species often are robust to forest management. Rosenberg and Raphael (1986) do not detect a negative response by small mammals to forest fragmentation in the Rocky Mountains, suggesting instead that deer mice (*Peromyscus maniculatus*) respond positively to some edge and clearcut measures. Sekgororoane and Dilworth (1995) and Bayne and Hobson (1998) also find deer mice associated with edges. Other studies suggest that deer mice and red-backed voles (*Clethrionomys gapperi*), two of the most common small-mammal species in eastern North America, are not adversely affected by the cumulative effects of stand interventions across forest landscapes (Yahner, 1992; Bayne and Hobson, 1998; Hayward et al., 1999). However, most studies of small-mammal populations do not consider the influence of landscape context independently of the effects of within-stand vegetation.

The spatial extents over which landscape context influences small-mammal populations will depend on the extents over which population processes of small-mammal species occur (e.g., Roland and Taylor, 1997). Krohne and Burgin (1990) and Bowman et al. (2000b) demonstrate that demographic variability in small mammal populations occurs over relatively

short distances (100 s of metres). These authors suggest that the variability is a result of processes such as predation, habitat selection, and competition occurring locally (i.e., within 100 s of metres). If such processes do indeed occur over small extents, then larger-scale landscape context should be relatively unimportant (e.g., Dickman and Doncaster, 1987). The objective of this paper was to assess whether small-mammal abundance was related to management-induced landscape context, when context was considered independently of within-stand vegetation and at different spatial extents.

2. Methods

Some aspects of the study design are also described by Bowman et al. (2000a, b). The study took place on the private industrial forest of Fraser Papers, in the Appalachian highlands of northwestern New Brunswick, Canada (47°N, 67°W). Upland sites were dominated by tolerant hardwood communities, with an overstory of sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britt.), and American beech (*Fagus grandifolia* Ehrh.). Lowland sites were dominated by black spruce (*Picea mariana* Mill.), white spruce (*P. glauca* (Moench) Voss), eastern white cedar (*Thuja occidentalis* L.), and balsam fir (*Abies balsamea* (L.) Mill.). We selected two study areas representing opposite ends of the continuum of forest management intensities: (1) a reference area, with relatively little management disturbance (i.e., <15% recent (<15 years) clearcut or softwood plantation); and (2) an intensively-managed area, where clearcuts and softwood plantations covered >50% of the landscape. We systematically placed sample points 1000-m apart, in a square (8×8) grid, providing two 4900 ha, square grids each with 64 sample points. For sampling reasons, points were not established within 50 m of roads or water bodies.

2.1. Small mammals

We trapped the sample points to estimate small-mammal abundance in spring and autumn, 1997. Five Victor Tin-Cat multiple-capture live traps (Woodstream, Lititz, PA, USA) were used to survey each sample point. One trap was placed at point centre, and

four other traps were placed at each cardinal direction, 35 m from centre. The five-trap array was designed to survey a 50 m radius around each point. All traps were placed in ‘most likely runway’ positions and prebaited for 3 days with oats and sunflower hearts. Traps were then set for four consecutive nights. Therefore, a single point took 7 days to sample: three nights of prebaiting and four nights of trapping. The number of sampling points precluded us from trapping all the points simultaneously. During each season, trapping spanned three seven-day periods. Captured animals were weighed, identified to species and gender, checked for reproductive condition, marked with a 1 g monel ear tag (National Band and Tag, Newport, KA, USA) and released. Our protocol was approved by the University of New Brunswick Animal Care Committee. Trapping success was expressed as number of individuals per species per point over four nights, and this was considered a relative index of abundance. Shrews were not marked and so trapping success for shrews was expressed as number of captures per point.

2.2. *Within-stand vegetation*

Within-stand vegetation characteristics were sampled at each point using three 10 m × 20 m quadrats. One quadrat was placed at the centre of the plot (offset 5 m to the west to avoid the effects of observer traffic at the point). Two other quadrats were placed 75 m from the centre at two of the following positions (selected randomly): north; southwest; southeast. Within each quadrat, trees ≥ 8 cm in diameter-at-breast-height (DBH) were counted, identified to species, and measured for DBH and decay class (1, healthy live tree; 9, decayed stump; Maser et al., 1979). Stems < 8 cm DBH were considered understory. Understory plants were sub-sampled on a 10 m × 2 m transect within the quadrats. All woody understory stems were identified to species and stratified by height: 0.5–1; 1–2; 2–4; 4–6; and > 6 m. The ground layer (leaf litter, herbs, bare ground, bryophytes, lichens, and graminoids) in each quadrat was measured by subjectively assigning a value from 0 to 5 (0, absent; 5, very abundant). Coarse woody debris was measured along the two, 20 m edges of each quadrat. Logs ≥ 8 cm diameter (mid-log) were tallied and measured for diameter, species (where possible),

and decay class (1, sound; 5, highly decayed; Maser et al., 1979). Vegetation surveys were completed during July and August of 1997.

2.3. *Landscape context*

Digital forest inventories, based on 1996 aerial photographs, were obtained from the land owner and were used to describe the forest landscapes. We used a Geographic Information System (GIS; Arc/Info and Arc/View) to develop landscape metrics. We wanted metrics that would describe the effects of forest management on the landscape, at a range of spatial scales. We reclassified the landscapes into six coarse patch types: tolerant hardwood; partially-cut tolerant hardwood (< 15 years since intervention), softwood, mixedwood, clear cut (< 15 years), and plantation (< 15 years; included the oldest available). Most plantations were scarified and had received an application of herbicide, so we did not separately measure these effects. Buffers of varying radii (100, 250, 500 m) were established around each sample point and within each buffer the composition of patch types was calculated, as a proportion. We calculated total edge (m) within each buffer (related to disturbance linearly; Hargis et al., 1998). To calculate edges, landscapes were dissolved into three cover types: (1) plantation+clearcut; (2) road; and (3) all other types. Only management-induced edges (roads, clearcut+plantation versus other forest types) were included. We also included separate variables measuring amount of road edge (m) and clearcut+plantation edge (m) within each buffer. In addition, the distance to the nearest road was measured for each sample point. As roads are a result of forest management, we felt that distance to roads should also be related to management disturbance. Finally, we calculated the number of patches within each buffer (a richness measure) and Simpson’s diversity index for each buffer.

2.4. *Data analysis*

A previous study (Bowman et al., 2000b) demonstrates that small-mammal populations at points 1000 m apart are not spatially autocorrelated. Therefore, we included all 128 sample points in parametric analyses.

A set of local vegetation variables was selected by performing a principle components analysis (PCA). We used the broken-stick model as a stopping rule for the PCA (Jackson, 1993), keeping the original vegetation variable that was most strongly loaded onto each PCA axis. We did not use the actual PCA scores because many vegetation variables exhibited non-normal distributions. Thus, the PCA was just an exploratory tool used to select variables.

Small-mammal data were counts, so we used poison regressions (from the family of Generalized Linear Models [GLMs]) to build optimal models relating the abundance of small mammals (by species and season) to the complete set of local vegetation characteristics. Optimal models were those explaining the most deviance in the response variable. Significance of these regression models was determined using analysis of deviance tables ($\alpha=0.05$). Deviance residuals from these regressions were saved and used as new variables, representing small mammal distributions independent of the effects of local vegetation. This new set of variables was regressed (using Gaussian GLMs; the deviance residuals had Gaussian distributions) against the set of landscape metrics, to measure the independent effects of landscape context on the distribution of small mammals. Compositional variables that were proportions were arcsine transformed.

3. Results

During 5120 trapnights, we made 1500 captures of >8 species (see Bowman et al., 2000a). We only carried out statistical analyses of the four most abundant species: deer mice; red-backed voles; short-tailed shrews, *Blarina brevicauda*; and woodland jumping mice, *Napaeozapus insignis*. Statistical analyses were not carried out on *N. insignis* data from autumn because of low abundance.

Analysis of 114 different sample points demonstrated that all four species were significantly related to within-stand vegetation characteristics. Depending on species and season, between 9 and 32% of the deviance in small-mammal distributions was explained by vegetation (Table 1).

Small-mammal species were distributed similarly among cover types in both spring and autumn (Table 2). Generally, red-backed voles and woodland jumping mice were most abundant in softwood sites, while deer mice and short-tailed shrews were most abundant in hardwood stands and in clear cuts. No species was abundant in plantations.

When the effects of within-stand vegetation were removed from small-mammal abundances, two species were significantly related to variables describing landscape context. In both spring and autumn,

Table 1
Results of generalized linear models relating vegetation variables to mammal abundances in northwestern New Brunswick^a

Species ^b	Spring 1997		Autumn 1997	
	Variable	Deviance (%)	Variable	Deviance (%)
<i>C. g.</i>	Softwood shrubs <1 m	13.3 ⁺⁺⁺	Spruce stems	14.5 ⁺⁺⁺
	Hardwood shrubs 2–4 m	5.3 ⁺	Hardwood shrubs >6 m	4.4 ⁺
	Balsam fir snags	5.7 ⁺	Softwood shrubs <1 m	2.3 ⁺
<i>P. m.</i>	Hardwood shrubs 4–6 m	3.8 ⁺	Beech stems	4.2 ⁺
	Balsam fir stems	6.5 ⁺	Sugar maple stems	7.0 ⁺⁺
			Beech shrubs 4–6 m	2.6 ⁺
<i>B. b.</i>	Hardwood shrubs 2–4 m	9.4 ⁺⁺	Balsam fir stems	2.8 ⁺
			Sugar maple shrubs <1 m	11.0 ⁺⁺⁺
<i>N. i.</i>	Total snags	15.6 ⁺⁺⁺	Hobblebush ^c shrubs <1 m	4.2 ⁺
	Yellow birch shrubs <1 m	10.1 ⁺⁺	Total stems	4.1 ⁺
	Coarse woody debris	6.0 ⁺	(No analysis)	

^a Variables are all counts and are listed in order of entry. Relationships are significant at: $p < 0.001$ ⁺⁺⁺; $p < 0.01$ ⁺⁺; or $p < 0.05$ ⁺. All significant relationships are positive. For all regressions, $N=114$.

^b *C. g.*, *Clethrionomys gapperi*; *P. m.*, *Peromyscus maniculatus*; *B. b.*, *Blarina brevicauda*; and *N. i.*, *Napaeozapus insignis*.

^c *Viburnum alnifolium* Marsh.

Table 2

Mean number of individuals ($\pm 95\%$ confidence interval) captured by season in major stand types during a small-mammal trapping project in northwestern New Brunswick in 1997^a

Species ^b	Season	Hardwood (N=43)	Softwood (N=18)	Plantation (N=13)	Clear cut (N=8)	Partial cut (N=10)
<i>C. g.</i>	Spring	0.7 \pm 0.5	1.9 \pm 1.2	0.1 \pm 0.2	0.3 \pm 0.3	0.6 \pm 0.6
	Autumn	1.5 \pm 0.8	4.3 \pm 1.8	0.4 \pm 0.4	1.4 \pm 1.3	0.7 \pm 0.5
<i>P. m.</i>	Spring	0.8 \pm 0.3	0.4 \pm 0.3	0.2 \pm 0.2	1.0 \pm 1.2	0.3 \pm 0.4
	Autumn	3.8 \pm 1.0	2.5 \pm 1.4	1.3 \pm 1.5	4.1 \pm 3.3	5.0 \pm 2.3
<i>B. b.</i>	Spring	0.5 \pm 0.3	0.1 \pm 0.2	0.2 \pm 0.3	0.4 \pm 0.4	0.0 \pm 0.0
	Autumn	2.5 \pm 0.8	1.6 \pm 0.7	0.7 \pm 0.5	1.9 \pm 1.2	4.7 \pm 3.2
<i>N. i.</i>	Spring	0.1 \pm 0.1	0.6 \pm 0.5	0.0 \pm 0.0	0.1 \pm 0.2	0.0 \pm 0.0
	Autumn	0.0 \pm 0.1	0.2 \pm 0.2	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0

^a The sampling design was systematic, so some trapping grids were intersected by >1 stand-type. These intersected samples were excluded from the summary.

^b *C. g.*, *Clethrionomys gapperi*; *P. m.*, *Peromyscus maniculatus*; *B. b.*, *Blarina brevicauda*; and *N. i.*, *Napaeozapus insignis*.

Table 3

Results of GLMs relating landscape context variables to mammal abundances in northwestern New Brunswick^a

Species ^b	Spring 1997		Autumn 1997	
	Variable	Deviance (%)	Variable	Deviance (%)
<i>C. g.</i>	Plantation (250 m) ^d	4.3 ⁻	Plantation (100 m) ^c	7.2 ⁻
<i>P. m.</i>	No significance		No significance	
<i>B. b.</i>	No significance		No significance	
<i>N. i.</i>	Softwood (100 m) ^c	4.8 ⁺	(No analysis)	

^a Mammal (response) variables are abundances with local vegetation trends removed through regression. Relationships are significant at: $p < 0.01$ ⁻ or $p < 0.05$ ⁺. Direction of significant relationships is indicated by + or - signs. For all regressions, $N = 114$.

^b *C. g.*, *Clethrionomys gapperi*; *P. m.*, *Peromyscus maniculatus*; *B. b.*, *Blarina brevicauda*; and *N. i.*, *Napaeozapus insignis*.

^c Variable calculated within a 100 m radius.

^d Variable calculated within a 250 m radius.

red-backed voles were negatively associated with the amount of plantation. The best model (i.e., most explained deviance) for this relationship was for a 250 m radius in spring and a 100 m radius in autumn (Table 3). Woodland jumping mice were positively associated with the amount of softwood within a 100 m radius of sampling points (Table 3). No species were significantly related to any edge variables at any radius, nor to the distance of the nearest road. Nor were there any significant relationships with the richness or diversity of patches.

4. Discussion

Our results were indicative of the resource generalism of many small-mammal species. Although

within-stand vegetation was always significantly related to species-specific small-mammal abundance, a relatively low amount of deviance was explained (between 9 and 32%; Table 1).

Landscape context was related to the distributions of two species: *C. gapperi* and *N. insignis*. Although context was important, it was never important at the largest radius of 500 m (Table 3). We believe that this is consistent with the suggestion of Krohne and Burgin (1990) and Bowman et al. (2000b) that processes occur locally to structure small-mammal populations in space. Bowman et al. (2000b) find *C. gapperi* and *N. insignis* populations spatially autocorrelated at scales of 275 m or less, depending on the landscape.

The negative relationship between *C. gapperi* and the amount of plantation accords with other studies that find red-backed voles to be negatively-related to

forest management indices. Mills (1995) finds western red-backed voles (*C. californicus*) to be more abundant in interiors than forest edges and similarly, Sekgororoane and Dilworth (1995) find that *C. gapperi* are most abundant in forest interiors compared to forest-clearcut edges. Although some studies do not indicate a negative association between red-backed voles and managed forests (e.g., Kirkland, 1990; Yahner, 1992; Bayne and Hobson, 1998), Nordyke and Buskirk (1991) suggest that *C. gapperi* is an indicator of old-growth conditions in the Rocky Mountains because of a positive relationship with decadent coarse woody debris. We also find a relationship between red-backed voles and coarse woody debris (Bowman et al., 1999; Bowman et al., 2000a) and this may explain, in part, why voles were negatively-related to plantations. Although young plantations might be suitable for voles (Parker, 1989), in our study area plantations had received site preparation (e.g., herbicide) that removed much of the structure and forage.

Woodland jumping mice were more abundant during spring in landscapes with softwood forest (Table 3). At a continental scale, the distribution of this species is related to the distribution of hemlock, spruce, and balsam fir (Banfield, 1984), and there is a microhabitat relationship between softwood species and woodland jumping mice (e.g., Vickery, 1981).

Our data do not support studies that find a positive relationship between small-mammal species (particularly deer mice) and edge (Rosenberg and Raphael, 1986; Sekgororoane and Dilworth, 1995; Bayne and Hobson, 1998). Deer mice in our study were related to hardwood understory variables in both spring and fall (Table 1). Hardwood shrubs are themselves often associated with edges, so an affinity by deer mice for shrubby sites could be the basis for the apparent relationship between deer mice and edge.

The study demonstrated that in managed forest, four small-mammal species were significantly related to local vegetation variables. Two of the species demonstrated weak relationships to landscape context at spatial extents of 100 and 250 m. Highlighted were the resource generalism of small mammals and the robustness of many small-mammal species in the face of intensive forest management. Further studies should be carried out to study red-backed vole

population structure in forests perforated by softwood plantations.

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