

# The spatial component of variation in small-mammal abundance measured at three scales

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**Abstract:** We studied small-mammal populations across a range of spatial scales to determine if they exhibited spatial variability that was independent of the distribution of vegetation. Between 1996 and 1999, systematic livetrapping surveys were conducted on nested grids at three scales: (1) extent (total area covered by a grid) = 4900 ha, grain (minimum space between sampling points) = 1000 m; (2) extent = 306 ha, grain = 250 m; and (3) extent = 31 ha, grain = 125 m. The four most abundant species were the red-backed vole (*Clethrionomys gapperi*), the short-tailed shrew (*Blarina brevicauda*), the deer mouse (*Peromyscus maniculatus*), and the woodland jumping mouse (*Napaeozapus insignis*). Small mammals exhibited spatial population structure over distances up to 250 m but not over 1000 m. There was a component of this population structure that appeared to be temporally and spatially dynamic, and that was not correlated with measured vegetation variables. We discuss processes that would create the observed metapopulation structure in seasonal landscapes.

**Résumé :** Nous avons étudié des populations de petits mammifères à plusieurs échelles spatiales pour déterminer si ces populations subissent une variabilité spatiale indépendante de la végétation. De 1996 à 1999, nous avons procédé au piégeage d'animaux vivants dans des grilles d'échantillonnage emboîtées, sur trois échelles : (1) étendue = 4900 ha, pas d'échantillonnage = 1000 m; (2) étendue = 306 ha, pas d'échantillonnage = 250 m; (3) étendue = 31 ha, pas d'échantillonnage = 125 m. Le Campagnol-à-dos-roux de Gapper (*Clethrionomys gapperi*), la Grande Musaraigne (*Blarina brevicauda*), la Souris sylvestre (*Peromyscus maniculatus*) et la Souris sauteuse des bois (*Napaeozapus insignis*) étaient les quatre espèces les plus abondantes. Les populations de petits mammifères avaient une structure spatiale à un pas d'échantillonnage de plus de 250 m, mais pas à un pas de plus de 1000 m. L'une des composantes de cette structure semblait dynamique en temps et en espace, mais n'était en corrélation avec aucune des variables reliées à la végétation. Nous examinons les processus qui pourraient être responsables de la structure observée dans les paysages saisonniers.

[Traduit par la Rédaction]

## Introduction

Spatial variability in population attributes has often been related to variability in resource quality (e.g., environmental control, habitat-suitability models, ideal free habitat selection; Whittaker 1956; Fretwell and Lucas 1970). However, Quinn and Dunham (1983) suggested that patterns are often due to multiple factors, including biotic processes such as predation and competition. For example, Krohne and Burgin (1990) demonstrated heterogeneity in the density of populations of the white-footed mouse (*Peromyscus leucopus*) within a forest that those authors perceived to be homogeneous. Krohne and Burgin's (1990) study and others (Anderson

1970; Krohne and Baccus 1985; Montgomery 1989; Cooke 1997) suggest that population parameters such as density, allelic frequencies, and survival rate can vary independently of the distribution of resources.

The idea that population parameters can vary in space independently of resources is not new, in fact it is implicit in many theoretical discussions of genetics and population regulation in small mammals (e.g., Hansson 1977; Anderson 1980; Lidicker 1988). However, the spatial scale over which such variability occurs has seldom been quantitatively addressed. Some authors have demonstrated that populations can fluctuate in abundance synchronously over large regions, a phenomenon that suggests the contribution of regionwide processes (e.g., Moran 1953; Myrberget 1973; Ranta et al. 1995; Steen et al. 1996). Conversely, small-mammal populations can exhibit heterogeneous densities over relatively short distances, i.e., hundreds of metres (Krohne and Burgin 1990; Bowman et al. 2000), which suggests the contribution of local, rather than regional, processes.

The development of spatial analytical techniques has allowed ecologists to model processes that vary in space (e.g., Legendre and Fortin 1989; Borcard et al. 1992; Rossi et al. 1992; Thomson et al. 1996). These techniques generally involve the description of spatial patterns. Patterns that have structure (i.e., are not random) can be considered synthetic models of underlying spatial processes, such as dispersal or predation (Legendre and Fortin 1989; Borcard et al. 1992).

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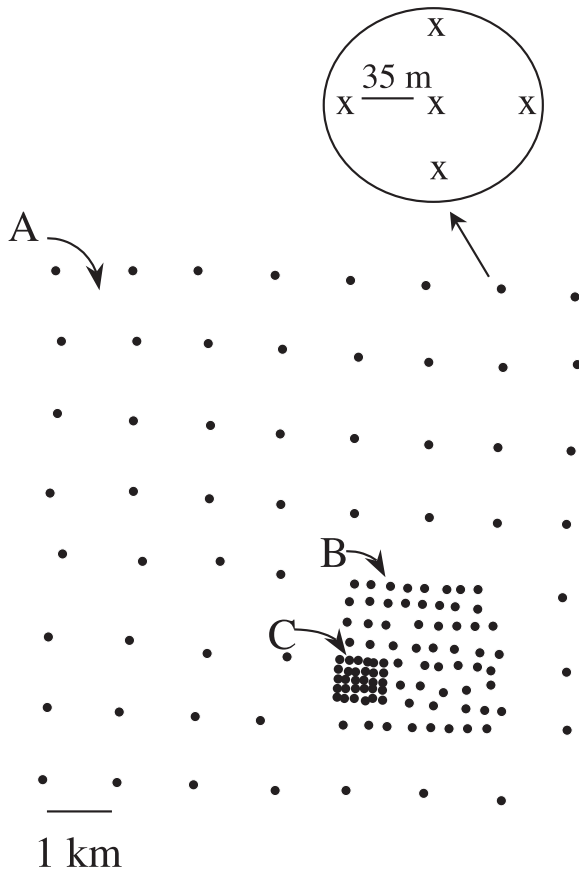
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**Fig. 1.** Layout of three study grids in a forest landscape in northwestern New Brunswick, Canada. Three nested scales were surveyed: A, 1000-m grain,  $8 \times 8$  sampling points, 4900-ha extent; B, 250-m grain,  $8 \times 8$  sampling points, 306-ha extent; C, 125-m grain,  $5 \times 6$  sampling points, 31-ha extent (see the text). Each survey point consisted of an array of five traps (inset). The topography of the site contributed to irregularities in the shape of grids.



As patterns have a scale, spatial analytical techniques can also be used to detect the scale of the underlying processes represented by spatial patterns (Legendre and Fortin 1989).

We tested the prediction that processes occurring independently of resource variation contribute to the distribution and abundance of small mammals. Our objectives were (i) to assess whether small-mammal populations exhibited non-random spatial patterns (i.e., structure) that were independent of the distribution of vegetation, and (ii) to determine the scale(s) over which this spatial structure occurred.

## Materials and methods

The study took place in the private industrial forest of Fraser Papers Inc. in the Appalachian forest of northwestern New Brunswick (47°N, 67°W). Upland sites were dominated by an overstory of sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*). Lowland sites were dominated by black spruce (*Picea mariana*), white spruce (*Picea glauca*), and balsam fir (*Abies balsamea*).

The study design was also described in detail by Bowman et al. (2000). The study was carried out in a 4900-ha forested landscape that was managed at low intensity for forest products (e.g., <15%

recent clearcuts or softwood plantations). A set of nested grids was used to sample the 4900-ha landscape for small mammals (Fig. 1). We use "grid" to refer to a systematic set of sampling points and "trap array" to refer to the traps placed at a single sampling point. The design of the grids can be described using "grain," which is the minimum space between sampling points, and "extent," which is the total area covered by a grid. The largest grid had a grain of 1000 m and an extent of 4900 ha ( $8 \times 8$  sampling points  $\times 8$  sampling points in a square grid, i.e., 64 sampling points). Nested within the large grid was a smaller grid with a grain of 250 m and an extent of 310 ha ( $8 \times 8$ , i.e., 64 sampling points) and a third grid with a grain of 125 m and an extent of 31 ha ( $5 \times 6$ , i.e., 30 sampling points). In total, 141 sampling points were spread systematically across the landscape within these grids.

At each sampling point an array of 5 Victor Tincat multiple-capture live traps (Woodstream Corp., Lititz, Pa., U.S.A.) was used to sample small-mammal populations (Fig. 1 inset). Traps were placed at the centre point and 35 m from the centre in each cardinal direction; each trap was placed in a "most likely runway" position within 2 m of the systematic location. Traps were prebaited for 3 days with oats and sunflower hearts and then set for 4 consecutive nights. The trapping protocol was carried out twice per annum, in spring (May–June) and autumn (August–September), from autumn 1996 until spring 1999. The large number of sampling points precluded us from trapping all the points simultaneously. Trapping on the largest grid (1000-m grain) spanned three 7-day periods, while the smaller grids were trapped within one or two periods. To check whether we had suitably controlled for temporal variation within samples, we tested for a relationship between small-mammal abundance and sampling date (within grids and seasons) and found no significant relationship. 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 Co., Newport, Kan., U.S.A.), and released.

Implicit in our study design was the assumption that sampled vegetation characteristics were correlated with the resources available to small mammals. Vegetation characteristics were measured using three  $10 \times 20$  m quadrats at each sampling point on all grids. 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 (randomly selected): north, southwest, and southeast. Within each quadrat, trees  $\geq 8$  cm 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 subsampled on a  $10 \times 2$  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 assigning a value from 0 to 5 (0 = absent, 1 =  $< 1\%$ , 2 =  $< 10\%$ , 3 =  $< 20\%$ , 4 =  $< 50\%$ , and 5 =  $\geq 50\%$ ) (Mueller-Dombois and Ellenburg 1974). Coarse woody debris was measured along the two 20-m edges of each quadrat. Logs  $\geq 8$  cm diameter (mid-log) were tallied and measured for diameter, species (where possible), and decay class (1 = sound to 5 = highly decayed; Maser et al. 1979). Vegetation surveys at each point were completed during July and August 1997.

Our design involved the assumption that neighbouring live-trapping arrays were related. In other words, we did not assume that sampling points within grids were independent. In this way, sampling points were intentionally pseudoreplicated, while varying the spatial scale, in order to determine the distance over which small-mammal populations exhibited spatial structure. Spatial terms were included as necessary surrogates for unmeasured spatial processes. Matrices of small-mammal abundance were related to vegetation and spatial location using canonical correspondence analysis

**Table 1.** Relative abundance (captures per 100 trap-nights) of four species of small mammals captured between 1996 and 1999 in northwestern New Brunswick, Canada.

	Autumn 1996	Spring 1997	Autumn 1997	Spring 1998	Autumn 1998	Spring 1999
<i>Clethrionomys gapperi</i>	5.17	6.38	9.92	7.24	18.83	7.56
<i>Peromyscus maniculatus</i>	0.81	4.13	22.30	3.05	3.62	6.54
<i>Blarina brevicauda</i>	4.24	2.04	9.63	1.83	17.76	13.87
<i>Napaeozapus insignis</i>	3.64	2.08	0.25	6.98	2.95	1.73

(CCA; ter Braak 1986). Small-mammal abundances were square-root transformed to dampen the effects of dominant species (e.g., ter Braak 1986; Palmer 1993; ter Braak and Šmilauer 1998). We used the method of partial constrained ordination (Borcard et al. 1992; Knick and Rotenberry 2000) to partition the variance in small-mammal abundance into four parts: (1) variation related to vegetation and independent of any spatial effects; (2) variation related to space and independent of any vegetation effects; (3) variation related to both spatial and vegetation effects (i.e., shared variance); and (4) unexplained variation.

A set of 20 local vegetation variables was selected from the more than 40 variables measured by performing a principal 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. Vegetation variables were often skewed and the PCA scores of these variables would have been unreliable. Therefore, we did not use the actual PCA scores; rather, the PCA was just an exploratory tool for selecting variables. Spatial structure was estimated using a set of two-dimensional geographical coordinates in a cubic polynomial (Borcard et al. 1992):

$$[1] \quad Z = b_1X + b_2Y + b_3XY + b_4X^2 + b_5Y^2 + b_6X^2Y + b_7XY^2 + b_8X^3 + b_9Y^3$$

where  $Z$  is spatial variation in small-mammal abundance and  $X$  is longitude and  $Y$  is latitude in Cartesian coordinates. The cubic polynomial was used because it has some ability to model nonlinearities. Each of the spatial terms in the polynomial was included as a separate variable. Our decision to use more vegetation variables than spatial variables was conservative: bias resulting from unequal numbers of variables would have underestimated the spatial, rather than the vegetation, component.

We used the same set of vegetation and spatial variables to conduct separate analyses at each of the three sampling scales. Partial constrained ordination was carried out using CANOCO 4 (ter Braak and Šmilauer 1998). For each small-mammal-abundance matrix, the optimal vegetation model was determined using the forward selection procedure available in CANOCO. Spatial models were determined in the same way. Partial ordinations were carried out by removing effects of the spatial model from the vegetation model and vice versa (e.g., Borcard et al. 1992). The significance of models was assessed using Monte-Carlo permutation tests with  $p < 0.05$ . Note, however, that with our approach, the significance of models was less important than the relative sizes of eigenvalues (explained variance) for spatial and vegetation models both within and across scales.

## Results

We conducted 16 320 trap-nights during the study. In autumn 1996, the 125 m grain grid was not trapped, so there were 119 sampling points spread over two grids (5 traps  $\times$  4 nights at each sampling point per season). During subsequent seasons, 141 sampling points were trapped. On rare

occasions, single sampling points had to be omitted because of inaccessibility. The most abundant species were the red-backed vole (*Clethrionomys gapperi*; 9.40 captures per 100 trap-nights), the short-tailed shrew (*Blarina brevicauda*; 7.89 captures per 100 trap-nights), the deer mouse (*Peromyscus maniculatus*; 7.66 captures per 100 trap-nights), and the woodland jumping mouse (*Napaeozapus insignis*; 2.78 captures per 100 trap-nights) (Table 1). These four, abundant species were included in the ordination analyses, with the exceptions of *P. maniculatus* from autumn 1996 and *N. insignis* from autumn 1997, owing to insufficient abundance during those seasons.

Data from each autumn during which we sampled demonstrated that vegetation models explained a significant amount of variation in the small-mammal-species matrix at every spatial scale (Table 2). However, the spatial models were only significant at the 125- and 250-m grains and never at the 1000-m grain. Little variation in small-mammal abundance was shared by the vegetation and spatial models (Table 3). No models lost significance during partial ordinations.

Findings based on the spring data were very similar to those from the autumn data. Vegetation models explained a significant amount of variation in the small-mammal-species matrix with the exception of the 1000-m grain during spring 1997 (Table 4). Spatial models derived from the spring analyses were always significant at the 125-m grain, but were only significant during spring 1999 at the 250-m grain. Spatial models from spring were never significant at the 1000-m grain (Table 4). As in the autumn, all models maintained significance during the partial ordinations, indicating that little of the variation in the small-mammal-abundance matrices was shared by the vegetation and spatial matrices (Table 3).

Regardless of season or scale, vegetation explained more variance in the small-mammal matrices than either the spatial or the shared (spatial-vegetation) components (Table 3, Fig. 2). The 95% confidence intervals (CI) for the mean variation in small-mammal matrices explained by vegetation overlapped across the three scales (Table 3). The spatial models explained more variance at the 125-m grain than either of the coarser grains (Table 3, Fig. 2).

## Discussion

Small-mammal populations in our study exhibited spatial variability that was independent of the distribution of vegetation. The spatial component of population structure was most important at our finest grain, 125 m (Fig. 2), but was also evident at a grain of 250 m. This result is consistent with our prediction that processes occurring independently

**Table 2.** Results of canonical correspondence analysis of small-mammal distributions in autumn (1996–1998) in northwestern New Brunswick.

Grain (m)	Year	<i>N</i>	Vegetation model	<i>F</i> <sup>a</sup>	Spatial model	<i>F</i> <sup>b</sup>
125	1996	—	na	—	na	—
	1997	30	Logs, mean decay class <i>Betula alleghaniensis</i> shrubs	3.58**	XY	2.56*
	1998	30	All coarse woody debris All stems	3.60**	Y <sup>2</sup>	5.06**
250	1996	64	<i>Picea</i> spp. stems	3.43**	XY <sup>2</sup>	3.48**
			<i>Acer saccharum</i> shrubs			
			All snags			
	1997	64	All coarse woody debris	3.03*	—	ns
			Logs, mean decay class			
	1998	64	All snags	4.59**	Y	4.38**
		All coarse woody debris		X		
1000	1996	61	<i>A. saccharum</i> stems	5.50**	—	ns
			<i>Fagus grandifolia</i> shrubs			
			Hardwood shrubs			
			<i>Viburnum alnifolium</i> shrubs			
			All snags			
	1997	59	<i>Picea</i> spp. stems	4.91**	—	ns
			All stems			
	1998	60	Logs, decay class 2	2.46*	—	ns
Softwood shrubs						
Softwood shrubs <i>Abies balsamea</i> stems						

**Note:** The small-mammal community included *C. gapperi*, *P. maniculatus*, *B. brevicauda*, and *N. insignis*; *P. maniculatus* was not included in autumn 1996 models and *N. insignis* was not included in autumn 1997 models because of low abundance. Variables are listed in order of entry into models. Unless otherwise indicated, vegetation variables are counts. na, not applicable. ns, not significant at  $p > 0.05$ .

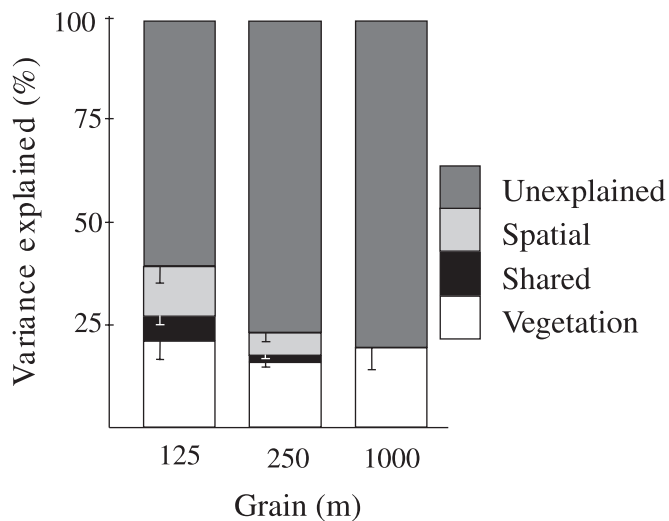
<sup>a</sup>Vegetation model; Monte-Carlo permutation test.

<sup>b</sup>Spatial model; Monte-Carlo permutation test.

\* $p < 0.05$ .

\*\* $p < 0.01$ .

**Fig. 2.** Variance in the abundance of small mammals in a forest landscape attributed to (i) an unexplained component; (ii) a spatial component (with vegetation effects removed); (iii) a shared spatial–vegetation component; and (iv) a vegetation component (with spatial effects removed). Amounts shown are means of samples taken during spring and autumn (1996–1999). Error bars indicate standard error. Sampling was carried out at three spatial scales (125-, 250-, and 1000-m grains).



of resource variation would contribute to the distribution of small-mammal populations.

There are other explanations for the patterns that we observed. There may have been resources that were unmeasured but contributed to the structure of the small-mammal populations. However, we were unable to find a potential resource that exhibited similar spatial patterns as the distribution of small mammals. We suggest that something other than just resource distribution was involved. For example, a time series of the spatial patterns of red-backed vole abundance revealed that while the scale of spatial structure was consistent, the actual patterns were, temporally, remarkably dynamic (Fig. 3). Not one site within the 125-m-grain grid was occupied by red-backed voles during every sampling. These voles may have been tracking an unmeasured, shifting resource through time, but we suggest, rather, a dynamic process of extinction and recolonization. Under this scenario, a combination of resource use and other biotic processes (such as winter mortality and predation) created a kind of metapopulation structure (e.g., Fig. 3). We envision a process whereby high winter mortality contributes to local extinctions and small spring populations. The summer growing season leads to a period of recolonization in the autumn. This recolonization will be somewhat stochastic within an area containing suitable resources, given potential randomness in the direction of dispersal. The extent of the spatial

**Table 3.** Results of partial constrained ordination (canonical correspondence) expressed as variance in small-mammal distributions explained (%) by vegetation (with spatial effects removed), spatial coordinates (with vegetation effects removed), and a shared spatial–vegetation component.

Matrix	Grain (m)	Autumn			Spring			Mean ± 95% CI
		1996	1997	1998	1997	1998	1999	
Vegetation	125	—	16	17	42	16	19	22.0±9.8
	250	18	15	21	23	18	12	17.7±3.1
	1000	49	28	8	0	30	15	21.5±11.2
Spatial	125	—	4	24	7	11	6	11.1±6.9
	250	6	0	10	0	0	6	3.6±3.3
	1000	0	0	0	0	0	0	0
Shared	125	—	5	<1	15	1	<1	4.2±4.9
	250	1	0	3	0	0	2	1.1±1.2
	1000	0	0	0	0	0	0	0

**Note:** The small-mammal community included *C. gapperi*, *P. maniculatus*, *B. brevicauda*, and *N. insignis*; *P. maniculatus* was not included in autumn 1996 models and *N. insignis* was not included in autumn 1997 models because of low abundance.

**Table 4.** Results of canonical correspondence analysis of small-mammal distributions in spring (1997–1999) in northwestern New Brunswick.

Grain (m)	Year	<i>N</i>	Vegetation model	<i>F</i> <sup>a</sup>	Spatial model	<i>F</i> <sup>b</sup>
125	1997	30	<i>Abies balsamea</i> stems	4.40**	XY	4.49**
			<i>Acer saccharum</i> stems			
			<i>A. saccharum</i> shrubs			
125	1998	30	<i>Betula alleghaniensis</i> shrubs			
			Softwood shrubs	2.49*	Y	3.65*
			All stems			
125	1999	30	Logs, decay class 4	3.09*	Y	2.30*
			<i>B. alleghaniensis</i> stems			
250	1997	64	Hardwood shrubs	2.72**	—	ns
			All stems			
			Logs, decay class 3			
250	1998	64	<i>A. saccharum</i> shrubs			
			All stems	4.11**	—	ns
			<i>A. saccharum</i> stems			
250	1999	64	Logs, decay class 1	3.07*	Y	5.25*
			Logs, decay class 5			
			Logs, mean diameter			
1000	1997	56	—	ns	—	ns
			All herbs	2.85**	—	ns
			Logs, mean diameter			
1000	1998	62	<i>Picea</i> spp. stems			
			All stems			
			All shrubs			
1000	1999	55	Softwood shrubs	4.11**	—	ns
			<i>Abies balsamea</i> stems			

**Note:** The small-mammal community included *C. gapperi*, *P. maniculatus*, *B. brevicauda*, and *N. insignis*. Variables are listed in order of entry into models. Unless otherwise indicated, vegetation variables are counts. ns, not significant at  $p > 0.05$ .

<sup>a</sup>Vegetation model; Monte-Carlo permutation test.

<sup>b</sup>Spatial model; Monte-Carlo permutation test.

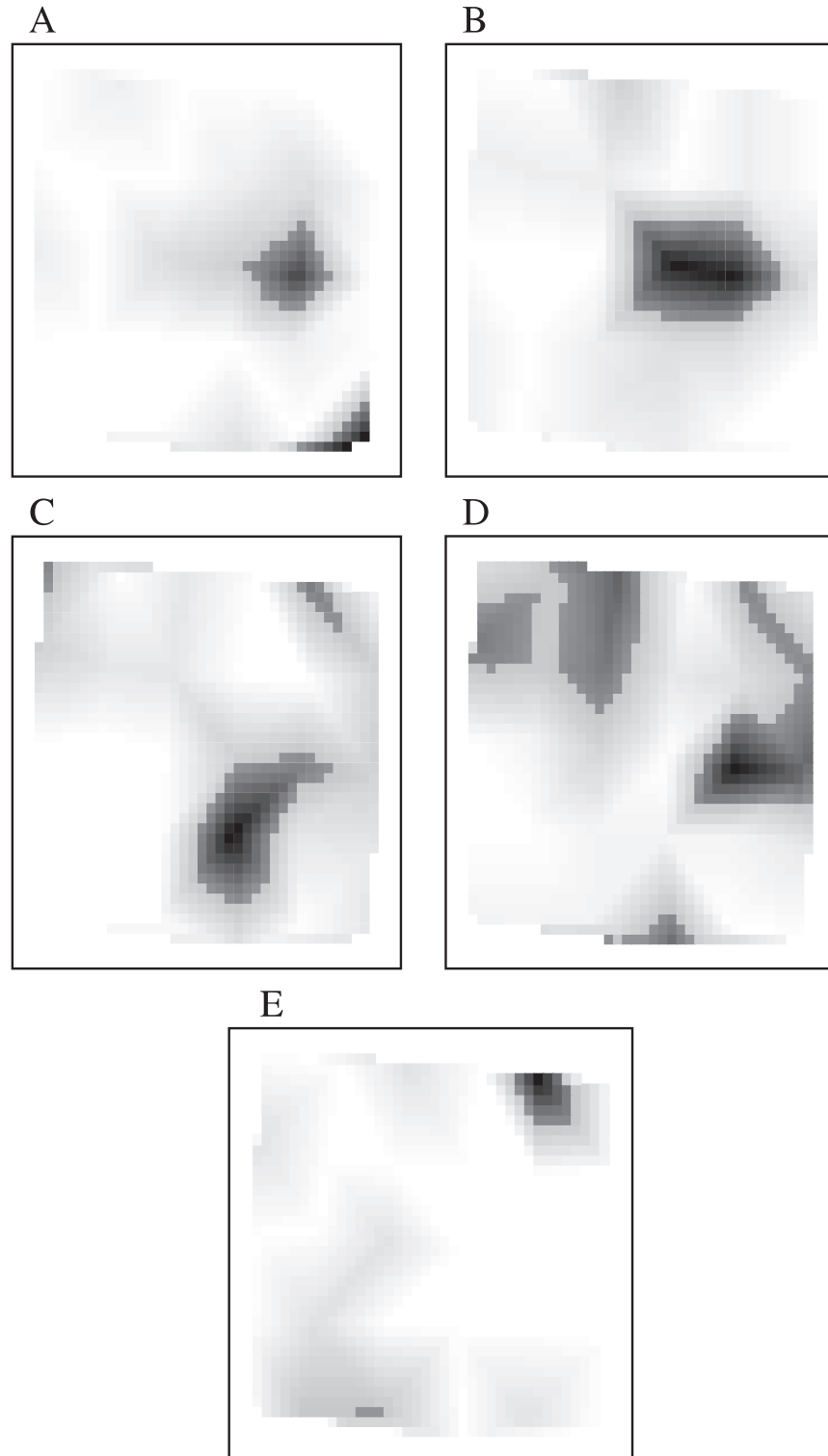
\* $p < 0.05$

\*\* $p < 0.01$ .

structure of recolonizing populations will be determined, in part, by the distances that dispersers travel (e.g., Krohne and Burgin 1990). For example, mean long-distance movements made by species in the present study ranged from 224 m (*C. gapperi*) to 370 m (*P. maniculatus*) (Bowman 2000). These dispersal distances are consistent with the spatial variation that we detected in small-mammal populations (e.g.,

Fig. 2). Thus, according to our speculation, mortality and dispersal interact to create temporally dynamic spatial structure within an area of potentially suitable resources (e.g., Fig. 3). Such a process would lead to high year-to-year variability in correlations between small mammals and vegetation for data collected over fine scales (relative to the present study). Temporal variability in habitat relationships

**Fig. 3.** Interpolated gray-scale maps showing the abundance of *Clethrionomys gapperi* during five consecutive trapping sessions in New Brunswick. Samples were taken on a 31-ha grid ( $5 \times 6$ ; 125-m grain) during spring 1997 (A), autumn 1997 (B), spring 1998 (C), autumn 1998 (D), and spring 1999 (E). Abundances range from 0 (white) to 12 (black) per survey point.



is a common finding in small-mammal studies (e.g., Grant 1976; Morris 1984; Vickery et al. 1989).

For each of the spatial scales at which we sampled, there was a large amount of unexplained variation in small-mammal abundance (Fig. 2), some of which may have re-

sulted from inadequate sampling of small-mammal, vegetation, and spatial matrices. For example, the spatial matrix was constrained to a cubic polynomial. However, unexplained variance is overrepresented in a CCA and is therefore hard to interpret (Okland 1999). This problem arises, in

part, because eigenvalues (the numerator in calculations of explained variance) are constrained to be  $<1.0$ , while total inertia (the denominator) has no such constraint. It is therefore impossible to explain all of the variance. Okland (1999) suggested that we ignore the unexplained component of partitioned variance. We think that it suffices to say that we were exhaustive in our sampling, and that a large unexplained component would be consistent with previous research that has demonstrated the resource generalism of the small-mammal species in our study (e.g., Grant 1976; Kozakiewicz 1995; Morris 1996). The four species in this study are all wide-ranging and exhibit a variety of habitat associations across their ranges (Dilworth 1984).

Small-mammal populations exhibited spatial structure over distances up to 250 m but not over 1000 m. We suggest a process whereby seasonal mortality and dispersal interact to create this temporally dynamic spatial structure within potentially suitable resources, or habitat. This process should lead to high yearly variability in small-mammal habitat-use patterns when measured over distances of a few hundred metres or less. In similar systems, we suggest that replicated grids should be  $>250$  m apart. Our findings may have implications for studies of small-mammal habitat ecology, particularly in seasonal environments. Standard sampling methodology (e.g., Smith et al. 1975) often assumes a more static spatial structure than we have detected. This assumption could lead to erroneous conclusions about habitat quality if populations are spatially and temporally dynamic.

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## References

- Anderson, P.K. 1970. Ecological structure and gene flow in small mammals. *Symp. Zool. Soc. Lond.* No. 626. pp. 299–325.
- Anderson, P.K. 1980. Evolutionary implications of microtine behavioural systems on the ecological stage. *Biologist*, **62**: 70–88.
- Borcard, D., Legendre, P., and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. *Ecology*, **73**: 1045–1055.
- Bowman, J. 2000. The spatial structure of small-mammal populations in a managed forest. Ph.D. dissertation, University of New Brunswick, Fredericton.
- Bowman, J., Forbes, G., and Dilworth, T. 2000. The spatial scale of variability in small-mammal populations. *Ecography*, **23**: 328–334.
- Cooke, J.L. 1997. A spatial view of population dynamics. In *Wildlife and landscape ecology: effects of pattern and scale*. Edited by J.A. Bissonette. Springer-Verlag, New York. pp. 288–309.
- Dilworth, T.G. 1984. The land mammals of New Brunswick. T.G. Dilworth, Fredericton, N.B.
- Fretwell, S.D., and Lucas, H.L., Jr. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheor.* **19**: 16–34.
- Grant, P.R. 1976. An 11-year study of small mammal populations at Mont St. Hilaire, Quebec. *Can. J. Zool.* **54**: 2156–2173.
- Hansson, L. 1977. Spatial dynamics of field voles *Microtus agrestis* in heterogeneous landscapes. *Oikos*, **29**: 539–544.
- Jackson, D.A. 1993. Stopping rules in principle components analysis: a comparison of heuristical and statistical approaches. *Ecology*, **74**: 2204–2214.
- Knick, S.T., and Rotenberry, J.T. 2000. Ghosts of habitats past: contribution of landscape change to current habitats used by shrubland birds. *Ecology*, **81**: 220–227.
- Kozakiewicz, M. 1995. Resource tracking in space and time. In *Mosaic landscapes and ecological processes*. Edited by L. Hansson, L. Fahrig, and G. Merriam. Chapman and Hall, London. pp. 136–147.
- Krohne, D.T., and Baccus, R. 1985. Genetic and ecological structure of a population of *Peromyscus leucopus*. *J. Mammal.* **66**: 529–537.
- Krohne, D.T., and Burgin, A.B. 1990. The scale of demographic heterogeneity in a population of *Peromyscus leucopus*. *Oecologia*, **82**: 97–101.
- Legendre, P., and Fortin, M.-J. 1989. Spatial pattern and ecological analysis. *Vegetatio*, **80**: 107–138.
- Lidicker, W.Z., Jr. 1988. Solving the enigma of microtine “cycles.” *J. Mammal.* **69**: 225–235.
- Maser, C., Anderson, R., Cromack, K., Jr., Williams, J.T., and Martin, R.E. 1979. Dead and down woody material. U.S. Dep. Agric. Agric. Handb. No. 553. pp. 78–95.
- Montgomery, W.I. 1989. Population regulation in the wood mouse, *Apodemus sylvaticus*. II. Density dependence in spatial distribution and reproduction. *J. Anim. Ecol.* **58**: 477–494.
- Moran, P.A.P. 1953. The statistical analysis of the Canadian lynx cycle. II. Synchronization and meteorology. *Aust. J. Zool.* **1**: 291–298.
- Morris, D.W. 1984. Microhabitat separation and coexistence of two temperate-zone rodents. *Can. Field-Nat.* **98**: 215–218.
- Morris, D.W. 1996. Coexistence of specialist and generalist rodents via habitat selection. *Ecology*, **77**: 2352–2364.
- Mueller-Dombois, D., and Ellenburg, H. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York.
- Myrberget, S. 1973. Geographical synchronism of cycles of small rodents in Norway. *Oikos*, **24**: 220–224.
- Okland, R.H. 1999. On the variation explained by ordination and constrained ordination axes. *J. Veg. Sci.* **10**: 131–136.
- Palmer, M.W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology*, **74**: 2215–2230.
- Quinn, J.F., and Dunham, A.E. 1983. On hypothesis testing in ecology and evolution. *Am. Nat.* **122**: 602–617.
- Ranta, E., Lindström, J., and Lindén, H. 1995. Synchrony in tetranoid population dynamics. *J. Anim. Ecol.* **64**: 764–776.
- Rossi, R.E., Mulla, D.J., Journel, A.G., and Franz, E.H. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. *Ecol. Monogr.* **62**: 277–314.

- Smith, M.H., Gardner, R.H., Gentry, J.B., Kaufman, D.W., and O'Farrell, M.H. 1975. Density estimations of small mammal populations. *In* Small mammals: their productivity and population dynamics. Edited by F.B. Golley, K. Petruszewicz, and L. Ryszkowski. Cambridge University Press, London. pp. 25–33.
- Steen, H., Ims, R.A., and Sonerud, G.A. 1996. Spatial and temporal patterns of small-rodent population dynamics at a regional scale. *Ecology*, **77**: 2365–2372.
- ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis in ecology. *Ecology*, **67**: 1167–1179.
- ter Braak, C.J.F., and Šmilauer, P. 1998. CANOCO reference manual and user's guide to CANOCO for Windows: software for canonical community ordination, version 4. Microcomputer Power, Ithaca, N.Y.
- Thomson, J.D., Weiblen, G., Thomson, B.A., Alfaro, S., and Legendre, P. 1996. Untangling multiple factors in spatial distributions, lilies, gophers, and rocks. *Ecology*, **77**: 1698–1715.
- Vickery, W.L., Iverson, S.L., Mihok, S., and Schwartz, B. 1989. Environmental variation and habitat separation among small mammals. *Can. J. Zool.* **67**: 8–13.
- Whittaker, R.H. 1956. Vegetation of the Great Smokey Mountains. *Ecol. Monogr.* **26**: 1–80.