

The spatial scale of variability in small-mammal populations

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We studied small-mammal populations across a range of spatial scales to determine which scales were relevant to demographic variability. We predicted that a scale of variability in population structure would occur at the scale of dispersal, which has previously been described as < 200 m for some small-mammal species. Systematic live-trapping surveys were conducted on nested grids at three scales: 1) extent = 4900 ha, grain = 1000 m; 2) extent = 306 ha, grain = 250 m; and 3) extent = 31 ha, grain = 125 m. Prior to the present study, small-mammal populations had not been systematically live-trapped across a similar range of scales. From 1996 to 1998, surveys were conducted on a landscape intensively managed for timber, and on a reference landscape. Spatial analysis of abundance data demonstrated that small-mammal populations (four species) exhibited positive spatial autocorrelation at distances of between 133 and 533 m depending on the species and the landscape. No higher-order population structure was detected. Thus, within the range of scales we sampled, variability in small-mammal abundance occurred over short distances (i.e., 133–533 m).

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Understanding the temporal and spatial scales at which organisms perceive and respond to their environment is a central issue in ecology (Wiens 1989), although there has been a tendency by ecologists to study many phenomena within a narrow range of scales (Brown and Roughgarden 1990). For example, much empirical small-mammal research is done at spatial extents of < 2 ha (e.g., Burt 1940, Smith et al. 1975). The small, replicated plots often used are essential for many questions, but due to their size, they are not well suited for understanding larger-scale patterns and processes.

In recent years, spatially explicit field studies have demonstrated that a number of small-mammal species exhibit structured population dynamics across geographical regions (e.g., Steen et al. 1996, papers in Krebs 1997, Ranta et al. 1997a, b). Structure in small-mammal populations can also occur over spatial extents smaller than regions (e.g., subpopulations and

metapopulations; Krohne 1997, Goodwin and Fahrig 1998). There is little empirical research at this sub-regional scale. Krohne and Burgin (1990) and Morris (1992) find that structure in small-mammal populations is, in part, a result of processes occurring at a scale of hundreds of metres. Morris (1992) detects a dispersal scale of 140 m for *Peromyscus*. Krohne and Burgin (1990) detect a scale of demographic heterogeneity in *P. leucopus* that is < 3 ha. Morris (1992) and Krohne and Burgin (1990) may be referring to the same process: *Peromyscus* populations are organised into small (hundreds of metres) patches. By patch, we mean an area of demographic homogeneity, or low variability. Krohne and Burgin's (1990) patchy structure is directly related to Morris' (1992) dispersal scale – dispersing animals must travel out of a patch to establish a territory (Krohne and Burgin 1990). Such patches are variously defined in the literature as demes (Anderson 1970,

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Lidicker 1975, Krohne 1997), operational demographic units (Merriam 1995), or subpopulations (Krohne 1997).

A spatially explicit design was used to assess how populations were organised at scales not previously assessed in a systematic way. Our objective was to detect the spatial scale (or scales) of demographic variability in small-mammal populations, thereby identifying patch structure within the populations. Again, we use the term patch to describe areas of low demographic variability. We refrain from more traditional terms like deme, because of the population genetics connotation (Anderson 1970). In future studies we will relate patches of low variability in mammal abundance to landscape structure: a species-based approach to defining landscape elements. The present study was exploratory, necessary because few current data exist for us to make strong inferences about how populations of the relevant species were distributed in space. We assumed that the findings of Krohne and Burgin (1990) and Morris (1992) (concerning *Peromyscus*) apply broadly to other species of similar size. Therefore, we

expected patchiness, or low variability, only at the finest grain in the study (125 m), which was finer than Morris' (1992) dispersal scale. We expected that our coarsest grain was too fine to detect any regional population dynamics (e.g., Steen et al. 1996).

Materials and methods

The study took place on the Private Industrial forest of Fraser Papers Inc., in the Appalachian forest of north-western New Brunswick (47°N, 67°W). Upland sites were dominated by an overstorey 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 *Picea glauca* (Moench) Voss, and balsam fir *Abies balsamea* (L.) Mill.

Our long-term objectives included understanding the response of small mammal populations to the structure of managed forests. Therefore, 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 yr) 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 (reference and managed) each with 64 sample points. Nested within these large grids were 8 × 8 grids with grains of 250 m (306 ha). In the reference area only, there was a third nested grid with a grain of 125 m (30 points, 5 × 6, 31 ha) (Fig. 1). For sampling reasons, points were not established within 50 m of roads or water bodies, so some irregularities existed in the shape of the grids. At the top end, our choice of scales was a logistical one; we could not survey > 4900 ha. The finer scales were chosen for biological reasons with the smallest of these finer than Morris' (1992) dispersal scale. To our knowledge, this project (and a paired project in Alberta; Corkum et al. 1999) was the first where small mammals were systematically live-trapped over a similar range of spatial scales.

We trapped the sample points to estimate small-mammal abundance in spring and autumn beginning in autumn 1996 for the reference area and spring 1997 for the managed area (Table 1). Five Victor Tin-Cat multiple-capture live traps (Woodstream Corp., Lititz, PA, USA) were used to survey each sample point. One trap was placed at point center, and four other traps were placed at each cardinal direction, 35 m from center (Fig. 1 inset). 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 three days with oats and sunflower hearts. Traps

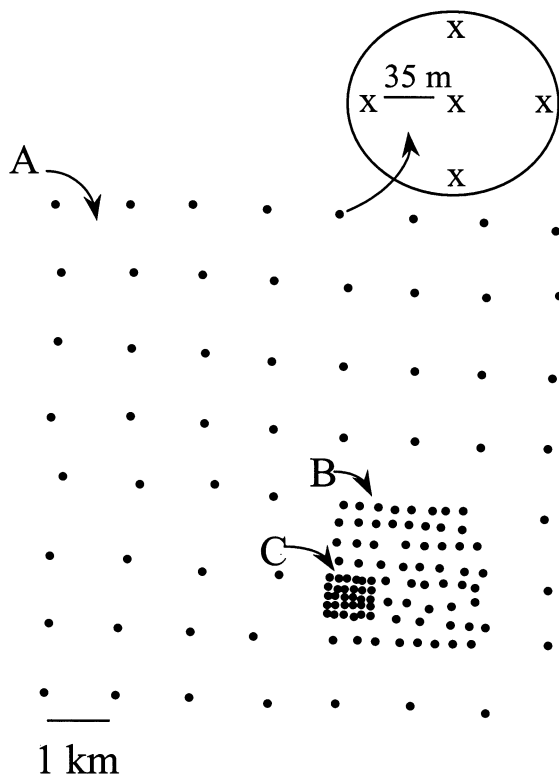


Fig. 1. Layout of three study grids on a reference forest landscape in northwestern New Brunswick, Canada. Three nested scales were surveyed: A = 1000-m grain, 8 × 8 points, 4900 ha extent; B = 250-m grain, 8 × 8 points, 306 ha extent; and C = 125-m grain, 5 × 6 points, 31 ha. Each survey point consisted of an array of five traps (inset). The study design was duplicated on an intensively managed forest landscape, with the exception of C, which was omitted.

Table 1. Live-trapping grids surveyed during autumn in northwestern New Brunswick. Three grids (125-m, 250-m, and 1000-m grains) were located in a reference landscape. Two grids (250 and 1000-m grains) were located in a managed landscape. Autumns when trapping was not conducted are indicated by "nt".

	1996	1997	1998
125-m reference	nt	t	t
250-m reference	t	t	t
1000-m reference	t	t	t
250-m managed	nt	t	t
1000-m managed	nt	t	nt

Table 2. Autumn capture rates (captures/100 tn) for small-mammal species captured in five study grids in northwestern New Brunswick. Listed in order of abundance in most abundant year.

Species	1996	1997	1998
* <i>Peromyscus maniculatus</i> Wagner	0.81	22.30	3.62
* <i>Clethrionomys gapperi</i> Vigors	5.17	9.92	18.83
* <i>Blarina brevicauda</i> Say	4.24	9.63	17.76
* <i>Napaeozapus insignis</i> Miller	3.64	0.25	2.95
<i>Microtus chrotorrhinus</i> Miller	0	0.16	0
<i>Mustela erminea</i> L.	0	0.14	0
<i>Microtus pennsylvanicus</i> Ord	0	0	0.07
<i>Synaptomys cooperi</i> Baird	0.04	0.02	0.02
<i>Zapus hudsonicus</i> Zimmerman	0	0.04	0
<i>Sorex</i> spp.	0	0.37	1.05

* indicates species selected for spatial analysis

were then set for four consecutive nights. Therefore, a single point took seven 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. Trapping on the largest grids (1000-m grain) spanned three seven-day periods, while the smaller grids were trapped within one or two periods and we assumed a negligible temporal drift in the samples. Captured animals were weighed, identified to species and gender, checked for reproductive condition, marked with a 1-g monel ear tag and released. Trapping success was expressed as number of individuals per species per point over four nights, considered a minimum estimate of abundance. Shrews were not marked and so trapping success for shrews was expressed as number of captures per point. Following Henttonen et al. (1985) we used autumn data (mid-August–mid-September) for studying spatial variability in small mammal populations.

Our statistical analysis of the small-mammal capture data was an initial, exploratory approach to describing the spatial structure of the sampled populations (Tukey 1980, Haining 1990). We used patterns of variability in abundance of small mammals as an index to demographic variability (Krohne and Burgin 1990). We assumed small-mammal populations were isotropic in their structure, and so we developed all-directional correlograms (Moran's I; Legendre and Fortin 1989) to

study patterns of spatial autocorrelation for species abundances in each of the three reference-area study grids (125-m, 250-m, and 1000-m grains). Then, correlograms were developed for the managed area and contrasted with the patterns of autocorrelation in the reference landscape.

As data were counts, distributions departed from normality, so we conducted our analyses on square-root transformed data. Most techniques for surface pattern analysis (i.e., structure functions: correlograms, semivariograms, and covariograms) require assumptions of normality and stationarity but are robust to departures. Haining (1990) suggests that structure functions are useful exploratory tools for non-normal data providing interpretations are limited. We chose correlograms over the more popular semivariograms (Meisel and Turner 1998) because they are standardised, facilitating comparison among correlograms. Both methods are comparable, in that calculating Moran's I yields a correlogram that is very similar to the inverse of a semivariogram (Meisel and Turner 1998). A second reason for using correlograms was that they allow an objective test of significance. Significance was determined using the Bonferroni procedure (Legendre and Fortin 1989), and because our approach was exploratory, we relaxed requirements for global correlogram significance to $\alpha = 0.1$ (Bonferroni-corrected) (Steen et al. 1996). Distance classes were established with approximately equal numbers of pairs in each class. Data analysis was conducted using S-Plus 4.0 (MathSoft, Seattle).

Results

From 1996 to 1998 we carried out 20980 multiple-capture trapnights, resulting in 5920 small-mammal captures. A range of species was captured, but we only conducted spatial analysis of the four most abundant species (Table 2). Populations of some species, especially deer mice, *Peromyscus maniculatus* Wagner, and woodland jumping mice, *Napaeozapus insignis* Miller, exhibited considerable inter-annual fluctuations and for these species spatial analysis was not conducted during the lowest years (Table 2).

All species exhibited heterogeneous distributions on all of the grids that were sampled. (Figs 2 and 3 are representative of the type of outputs available from our spatial analysis approach). However, we did detect significant positive spatial autocorrelation, which is an indication of the scale of patchiness, or low variability (Legendre and Fortin 1989). On the reference landscape during the autumn of 1997, red-backed vole, *Clethrionomys gapperi* Vigors, populations exhibited no autocorrelation (i.e., high variability) at the two largest scales (grains = 1000 and 250 m). At the finest grain (125 m),

voles exhibited significant positive autocorrelation at 133 m (Fig. 2). Deer mice populations were also heterogeneous on all grids; however, they exhibited a coarser-grained structure (than voles) with positive autocorrelation at 270–275 m (Fig. 3). We note here that correlogram distance classes were not exactly equal to the operational grain sizes (e.g., 133 vs 125 m) because of small irregularities in the shape of the grids.

Table 3 summarises the results of our spatial analyses for all species, landscapes, and years. There was no significant autocorrelation at the coarsest grain (1000 m), either in the reference or managed landscapes.

Depending on species and landscape, autocorrelation was detected at distances ranging from 133 to 533 m (Table 3). Significant patchiness was detected on the managed landscape for more species, and for larger distance classes than on the reference landscape at the mid-sized grain of 250 m (Table 3, Fig. 4).

Discussion

In this study we systematically sampled small-mammal populations over a broad range of spatial scales. Popu-

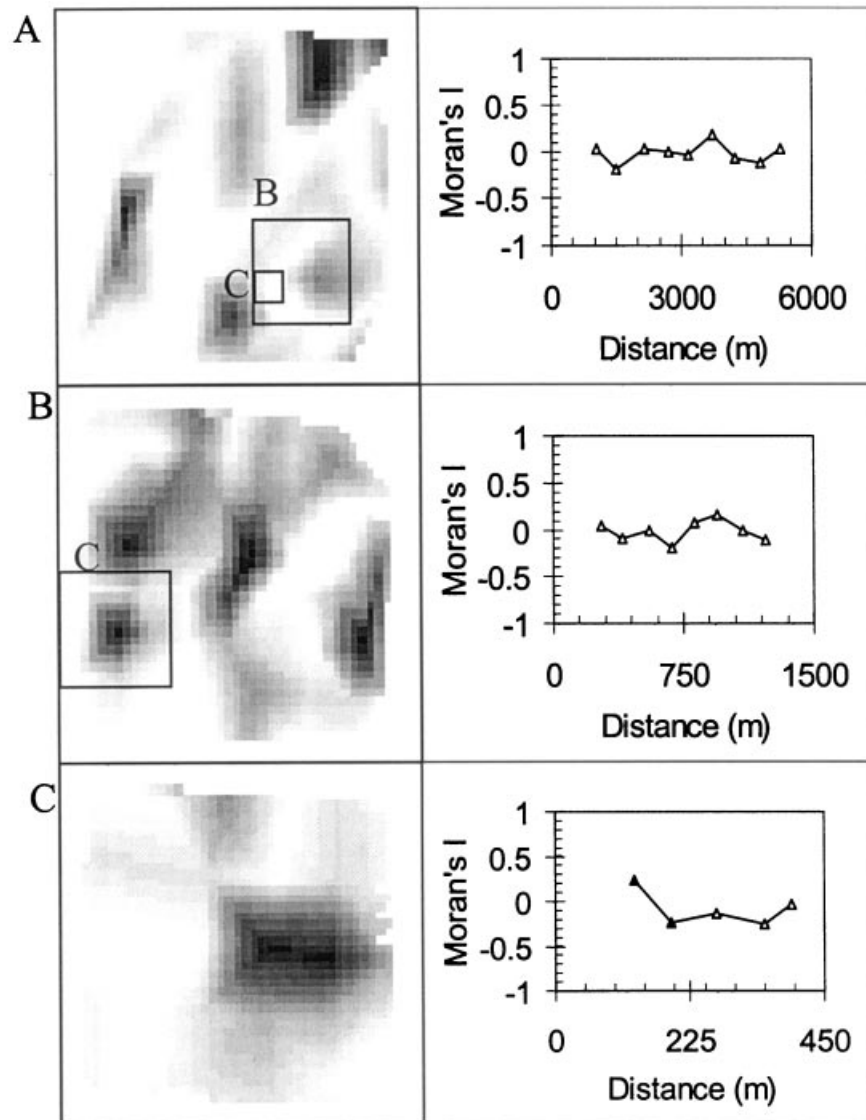


Fig. 2. Interpolated gray-scale maps and correlograms for autumn abundance of *Clethrionomys gapperi*, sampled at three spatial scales in a reference forest in New Brunswick. Three, nested survey grids are represented by: A (1000-m grain, 8 × 8 points, 4900 ha extent); B (250-m grain, 8 × 8 points, 306 ha extent); and C (125-m grain, 5 × 6 points, 31 ha extent). Abundance data range from 0 (white) to 12 (black) per survey point. Filled correlogram symbols indicate: 1) global correlogram significance; and 2) distance classes with significant autocorrelation.

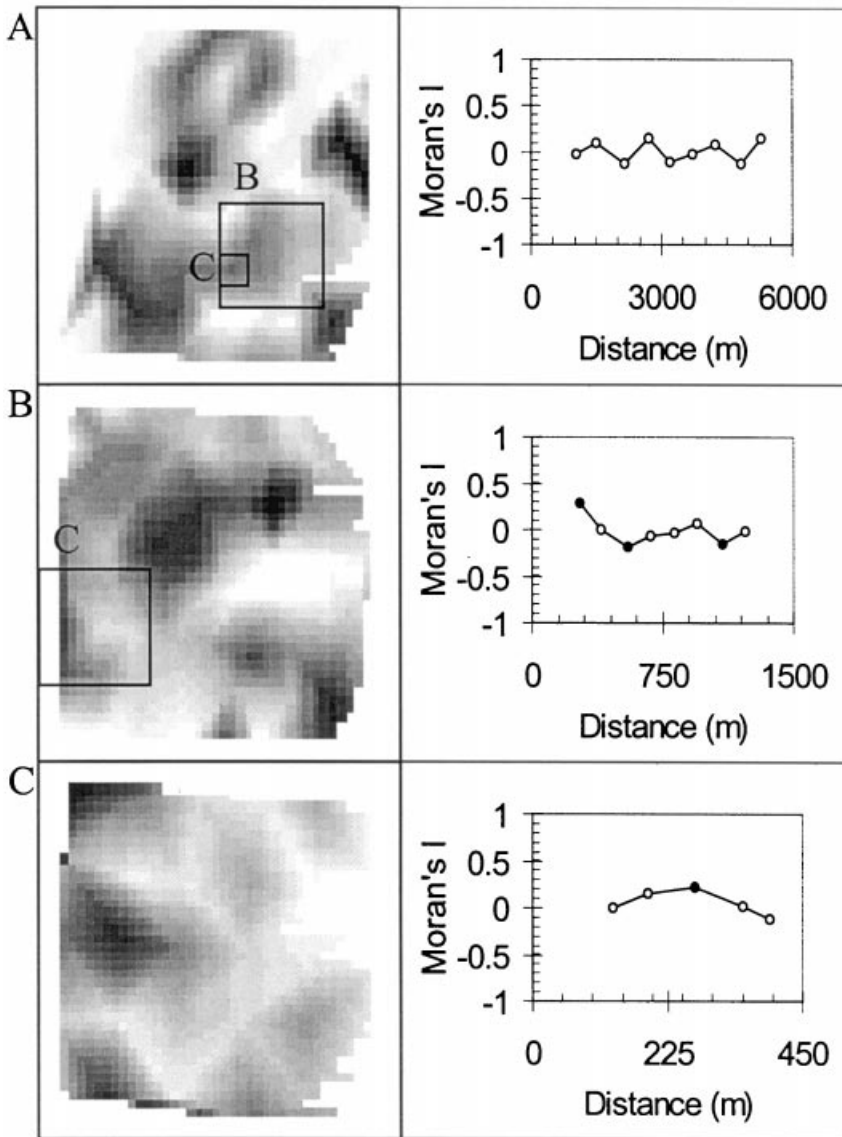


Fig. 3. Interpolated gray-scale maps and correlograms for autumn abundance of *Peromyscus maniculatus*, sampled at three spatial scales in a reference forest in New Brunswick. Three, nested survey grids are represented by: A (1000-m grain, 8 × 8 points, 4900 ha extent); B (250-m grain, 8 × 8 points, 306 ha extent); and C (125-m grain, 5 × 6 points, 31 ha extent). Abundance data range from 0 (white) to 15 (black) per survey point. Filled correlogram symbols indicate: 1) global correlogram significance; and 2) distance classes with significant autocorrelation.

Table 3. Distance classes (m) of positive autocorrelation from globally significant correlograms for small-mammal populations captured in autumn on five study grids in the forests of northwestern New Brunswick. A reference landscape contained three grids (125, 250, and 1000-m grains) and a managed landscape contained two (250 and 1000-m grains). All grids were surveyed in 1996 (96), 1997 (97), and 1998 (98) unless indicated by "nt" (not trapped). A hyphen "-" indicates that the correlogram was not globally significant.

	Reference landscape									Managed landscape					
	125-m			250-m			1000-m			250-m			1000-m		
	96	97	98	96	97	98	96	97	98	96	97	98	96	97	98
<i>C. g.</i>	nt	133	133	-	-	-	-	-	-	nt	267	267	nt	-	nt
<i>P. m.</i>	nt	270	350	-	275	275	-	-	-	nt	267	267	nt	-	nt
<i>B. b.</i>	nt	-	-	-	-	-	-	-	-	nt	533	-	nt	-	nt
<i>N. i.</i>	nt	-	270	-	-	275	-	-	-	nt	-	267	nt	-	nt

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

lations of small mammals were heterogeneously distributed on all grids (e.g., Figs 2 and 3). The results are supported by finer-scale research suggesting that many population processes occur locally (e.g., Patton and Feder 1981, Adler 1987). In our study, positive autocorrelation occurred at distances ranging between 133 and 533 m, depending on the species and the landscape (Table 3). The demographic variability in our study may have been related to: 1) the dispersal scale of 140 m for *Peromyscus* detected by Morris (1992); and 2) the 3-ha scale of demographic heterogeneity detected by Krohne and Burgin (1990), also for *P. leucopus*. While we studied different species, it is reasonable that similar processes were occurring. We suggest that dispersal operates at the same scale as demographic variability – it is exactly this variability that dispersers are trying to exploit.

Dispersing individuals seek vacant territory (Lidicker 1975, Krohne and Burgin 1990). This speculation raises a testable prediction: species with coarser spatial variability in population structure should disperse farther than species with finer spatial variability.

Our inability to detect any larger-scale patchiness suggests that, within the range of scales we studied, fine-scale (133–533 m) variation in resources, competition, and/or predator abundance affected the structure of the small-mammal populations. Thus, larger-scale patterns were an aggregate of the fine-scaled variation. At even larger, regional scales, spatially-structured population fluctuations can occur in some species (e.g., Steen et al. 1996, Ranta et al. 1997a, b), suggesting a level of organisation beyond the local dynamics considered in our study (e.g., Goodwin and Fahrig 1998).

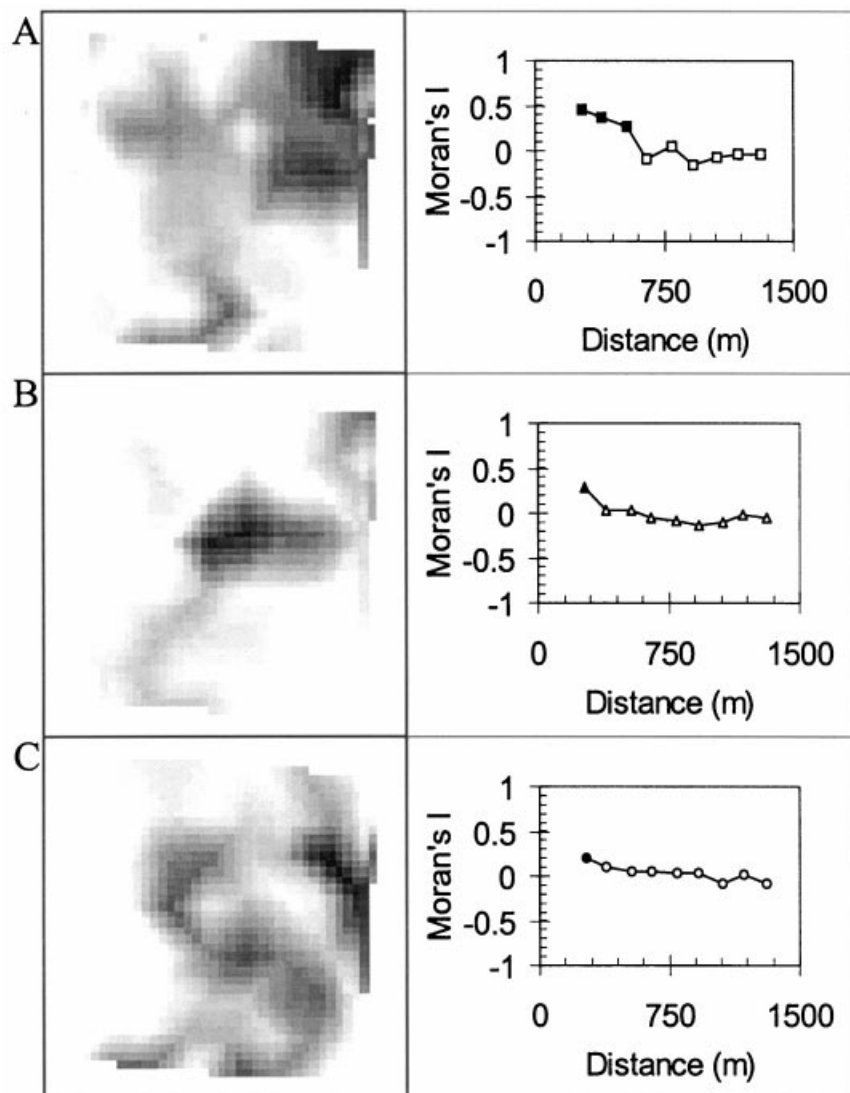


Fig. 4. Interpolated gray-scale maps and correlograms for autumn abundance of three small-mammal species in an intensively managed forest in New Brunswick, sampled on a systematic grid (250-m grain, 8×8 points, 306 ha extent). The three species are: *Blarina brevicauda* (A), *Clethrionomys gapperi* (B), and *Peromyscus maniculatus* (C). Abundances range from 0 (white) to 11 (black) individuals per point. Filled correlogram symbols indicate: 1) global correlogram significance; and 2) distance classes with significant autocorrelation.

Much of the spatial structure that we detected in our small-mammal data might be explained by structure in available resources. We will conduct future analyses to address this question; however, it is expected that some of the demographic variability occurred independently of habitat structure. Krohne and Burgin (1990) detect demographic heterogeneity in *P. leucopus* populations within apparently homogeneous hardwood stands, and we have observed demic structure in red-backed vole populations within much larger, (apparently) uniform softwood stands (Bowman et al. 1999).

Krohne and Burgin (1990) suggest that fine-scaled population aggregates (or patches) vary independently in space and time, depending on the abundance of resources or predators, which themselves fluctuate locally in space and time. Single patches are regulated by a single, dominant factor, but at the scale of the metapopulation, multiple factors regulate populations (Lidicker 1988). This may explain the difficulty researchers have had in trying to relate single factors to population regulation in small mammals (Krohne and Burgin 1990). This also may contribute to the low proportion of variance explained in many small-mammal habitat use studies and we cannot refute it with our data.

Our cross-scale design and analysis demonstrated that small-mammal populations exhibited spatial variability at distances of between 133 and 533 m. The approach was useful for exploring the data, raising some questions about the spatial structure of small-mammal populations. In particular, one testable prediction was raised: species with coarser spatial variability in population structure should disperse farther than species with finer spatial variability.

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