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On the roles of time, space and habitat in a boreal small mammal assemblage: predictably stochastic assembly

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Ecologists continue to debate the roles of deterministic versus stochastic (or neutral) processes in the assembly of ecological communities. The debate often hinges on issues of temporal and spatial scale. Resolution of the competing views depends on a detailed understanding of variation in the structure of local communities through time and space. Analyses of twelve years of data on a diverse assemblage of 13 boreal small mammal species revealed both deterministic and stochastic patterns. Stochastic membership in the overall community created unique assemblages of species in both time and space. But the relative abundances of the two codominant species were much less variable, and suggest a significant role for strong interactions that create temporal and spatial autocorrelation in abundance. As species wax and wane in abundance, they are nevertheless subject to probabilistic rules on local assembly. At the scales I report on here, poorly understood large scale processes influence the presence and absence of the majority of (sparse) species in the assembly. But the overall pool of species nevertheless obeys local rules on their ultimate stochastic assembly into groups of interacting species.

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All ecological communities are dynamic in space and time. But the roles of short term vs long term processes are poorly understood, and the relative importance of local vs regional effects is largely unresolved (Ricklefs and Schluter 1993). Recent models have explored the consequences of local colonization and extinction (Hubbell 2001) as well as source–sink dynamics (Mouquet and Loreau 2003) in metacommunities (Wilson 1992, Holt 1993), but empirical tests are either lacking or support competing alternatives (McGill 2003, Nee and Stone 2003). And, despite two decades of analysis and counter-analysis, the importance of random vs predictable assembly is also unresolved, as is the influence of stochastic vs deterministic processes (Brown et al. 2000, 2002, Stone et al. 2000). While some ecologists continue to work productively on mechanisms of coexistence (Kotler and Brown 1999, Eccard and Ylönen 2003, Ylönen and Kotler 2003, Ziv and Kotler 2003), many either do not study communities, or work at macroecological scales where local and short term effects represent only background noise in community assembly (Brown, 1995, Maurer 1999, Gaston and Blackburn 2001, Hubbell 2001, McGill 2003, McGill and Collins 2003, Nee and Stone 2003).

Others, harboring no apparent bias to either school, have improved our understanding by studying community assembly with theory (Post and Pimm 1983, Drake 1990, Pimm 1991, Law and Morton 1993, Luh and Pimm 1993, Morton et al. 1996, Lockwood et al. 1997) and with experiments on complex systems (Drake 1991, Drake et al. 1993, Lawler 1993, Fargione et al. 2003; see Drake et al. 1996, Samuels and Drake 1997, Weiher and Keddy 1999a, and Chase 2003 for many additional examples of both theory and experiment). The emerging

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consensus is that the assembly of any single community occurs through a variety of external constraints (e.g. environmental filters on regional species pools) and intrinsic processes (e.g. species interactions) in variable environments (Weiher and Keddy 1999b, Chase 2003). Membership in a given community will thereby be contingent on the potential pool of colonizing species, on the constraints and stochastic effects that influence colonization, persistence, and extinction, on whether species interactions lead to single or multiple basins of attraction, and on the temporal and spatial dynamics modifying all of these events (Belyea and Lancaster 1999). One (very difficult) way to assess the relative importance of these differing influences would involve tracking the actual trajectories of community dynamics through time (Samuels and Drake 1997). But there is also accumulating evidence that higher level "topological rules" act to limit community membership (Fox 1987, 1999, Drake et al. 1999, Bellwood et al. 2002, Fargione et al. 2003, Gillespie 2004). Such rules can be revealed by identifying repeated patterns at levels of organization above species (such as functional groups, Samuels and Drake 1997).

Regardless where individual ecologists fit into the debates on null vs deterministic assembly, neutral theory, or pattern vs process, no-one is likely to deny that species co-occur, that they interact through a myriad of direct and indirect pathways, and that the presence and abundance of some species influence those of others. But most of our understanding of local processes is based on studies and experiments of short duration, rather than longer term analyses of local dynamics. Exceptions include relatively long data series on northern mammals, both in North America (Vickery et al. 1989, Fryxell et al. 1998, Krebs et al. 2001, 2002) and in northern Europe (Henttonen et al. 1985, Marcström et al. 1990, Oksanen and Oksanen 1992). Detailed analyses of the long term data often imply competitive and other interactions among species, but mechanisms of coexistence and assembly remain relatively unexplored.

Theory, and studies including habitat, suggest that northern small mammal assemblages may often be structured, and assembled probabilistically, along habitat gradients (Morris 1983, 1996, Vickery et al. 1989, Morris and Knight 1996). The theory, based on consumer–resource models (MacArthur 1972, Tilman 1982), makes two key assumptions. 1) Different habitats support different mixtures of resources. 2) The differences in resource requirements of members within a single guild are less than the differences among guilds.

The proportion of resource space along a habitat gradient that is available to species in two-or-more guilds will thereby exceed that of any pair of species within a single guild. Stable points of coexistence for members of different guilds are thus more probable than for members of the same guild. The resulting assembly rule dictates that species entering a community will tend to represent different guilds until all guilds are present, before the rule repeats (Fox 1987, Fox and Brown 1993). We tested the theory on boreal rodent assemblages living along cutover-forest transects and confirmed all of the theory's predictions (Morris and Knight 1996). Subsequent studies with mammals (Fox 1999) and plants (Fargione et al. 2003) have confirmed the consumer–resource mechanism.

Our previous work was based on a series of assembly snapshots collected during one month of intense spatial sampling along 18 different transects. Each transect bisected recent cutovers and adjacent forest stands dominated by either coniferous or hardwood trees. The design maximized our ability to capture habitat's signal in community assembly, but had no ability to assess temporal variation. Here, I take the opposite tact of assessing two "photo-albums" containing temporal sequences of community snapshots. One sequence represents a 12 yr series of small mammal assemblages collected on eight sampling grids in a single forest stand. The other sequence represents an overlapping 6 yr series collected along four transects located in the same regional landscape. My objective is to merge spatiotemporal variation in a single analysis to sort out the relative contributions of stochastic versus deterministic processes on community assembly. Though the sampling intervals are too course to track the trajectories of individual assemblies, they nevertheless reveal the "location" of each assembly at different times and places.

To visualize the problem I wish to address, imagine that you have sampled a community of species across a variety of temporal and spatial scales. Now imagine that you use the identity and relative abundances of species to calculate an index of community similarity for each one, and plot the results as a three-dimensional graph (Fig. 1, most likely on a logarithmic scale). Against the broad background of temporal and spatial variation represented in Fig. 1, the most similar communities occur where space and time are funnelled toward "here and now". Through time, communities change in response to local conditions such as interactions among species, stochastic dynamics, ecological succession, and local invasions of new species. On longer time scales, communities vary with expansion and contraction of geographical ranges, extinctions, and speciation. Through space, communities reflect effects such as differences in habitat, differences in the mobility of potential colonists, and at large scales, differences in geographical ranges and biological provinces.

The "funnel" of community similarity is not fixed. It stretches and shrinks as community similarity is pushed, pulled, and tugged by the winds of change. As it does so, much of the variability that we see in communities will occur around its smallest tip representing the small

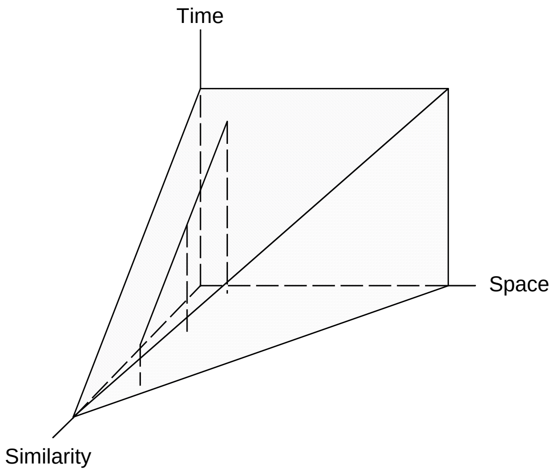

Fig. 1. An idealized illustration of how the similarity of ecological communities varies through space and over time. Points of intersection between the vertical dashed lines and the triangular upper surface represent the community similarity that might be observed through time at a single point in space. Time and space, in this illustration, are assumed to be independent. Community similarity in a study that includes both will be represented by different planes in the time–space continuum. In real systems, the temporal surface will undulate when communities change quickly in time; the spatial surface will vary where communities encounter discontinuities in space.

spatial and temporal scales of most ecological studies. What is here today may be gone tomorrow. No wonder that it is so difficult, at this scale, to detect pattern. Yet if it is process that we are interested in, the dynamic parts of the time and space continuum are exactly where we should concentrate our research. If it is pattern that dominates our interest, we should work at the much larger scales where broad features of communities emerge across huge expanses of time (palaeontology/phylogenetics) and space (biogeography). It is intriguing, nonetheless, that functional rules of species assembly also appear to operate at global biogeographical scales (e.g. for reef fish, Bellwood et al. 2002) even though the composition of those communities can be driven by dispersal from centers of adaptive radiation (Mora et al. 2003).

Studies along habitat gradients in space are most likely to reveal any more or less predictable rules of community assembly related to resource competition, habitat selection, and dispersal, but against a potentially dizzying background of stochastic dynamics. Studies through time are most likely to reveal the stochasticity of populations that may, nevertheless, yield relatively stable configurations of species. Thus, I concentrate on evaluating the temporal dynamics of a diverse small mammal assemblage, but with the objective of assessing whether deterministic processes related to small scales of habitat variation can be heard above the din of stochastic noise.

I begin by introducing the northern mammal assemblage and describe how we can use multinomial logistic regression as a tool to investigate spatial and temporal patterns in its assembly. The analysis is predicated on an ability to properly identify groups of samples based only on the small mammal assemblage. When groups of samples are represented by unique combinations of species, they will be classified easily to their proper positions in time and space. On the other hand, both static and noisy communities will exhibit low rates of classification because the samples lack spatial or temporal patterns. Communities with complex temporal or spatial correlations (Ranta et al. 1999, Lundberg et al. 2000) will yield intermediate classification rates because the range of possible associations is greater than for unique assemblies, and less than for random associations. I critique the sampling protocol, interpret the analyses in the context of the roles that time, space, and habitat play in the structure of ecological communities, then reconfirm the pattern of rodent assembly. I conclude by examining how repeated probabilistic rules of local assembly can be reconciled with the emerging unified theory of community ecology.

Methods

Beginning in 1991, my assistants and I have live-trapped and released small mammals during the summer on eight 1 ha study plots, as well as along four 390 m transects (starting in 1992), in Canada's boreal forest approximately 100 km north of Lake Superior (48°55′N, 89°55′W). The forest is a heterogeneous mixture of natural-origin conifer (jack pine, *Pinus banksiana*, black and white spruce, *Picea mariana*, *Picea glauca*, balsam fir, *Abies balsamea*), hardwood (predominantly trembling aspen, *Populus tremuloides*, and paper birch, *Betula papyrifera*) and mixedwood stands. A growing number of extensive clearcut blocks, most of which have received post harvest interventions (scarification with either aerial seeding or hand-planted conifer seedlings), are interspersed throughout the area. Appendix 1 describes the sites, their spatial scale, and field methods.

Testing for the effects of time, space, and habitat

My small mammal data represent samples collected during different years, at different places (e.g. distant vs near transects), at different scales (plots vs the forest segment of transects), and in different habitats (plots vs full transects including both forest and cutover segments). But the overall design, reflecting the logistic and other constraints of field work, is unbalanced. How can we partition the relative importance of each component on small mammal community assembly? I reasoned as follows: Imagine that we can classify, objectively, the different samples of small mammal assemblages according to year, location, scale, and habitat. Patterns in the classification can then be used to infer the relative importance of time, space, and habitat to the underlying rules that govern community assembly.

I chose multinomial (some prefer the term “polytomous”) logistic regression (MLR) as a suitable tool to classify assemblages. In a multinomial logistic regression,

$$\log\left(\frac{P_i}{P_j}\right) = B_{i0} + B_{i1}X_1 + B_{i2}X_2 + \cdots + B_{in}X_n \tag{1}$$

where the left hand term represents the natural log of the odds that an observation belongs to category i compared to category j (the “logit”; e.g. year 1 compared to year j), B is the set of logistic regression coefficients (one set for each logit), and X represents the set of independent (species) variables (Norušis 1999). Independent variables can be either continuous or categorical (I use both). The analysis can be used to explore the statistical contribution of different variables to the logits, as well as to calculate the probability that an observation belongs to a particular group. Logistic regression is more forgiving of distributional assumptions than many other classification approaches (e.g. discriminant functions analysis, Norušis 1999). My main interest here is to use the analysis as an objective means to classify assemblages into different a priori groupings (year, place, scale, and habitat).

I used the number of different individuals captured in a year as an initial estimate of the relative abundance of each species. I summed the total number of small mammal captures for each plot and transect for each year, then calculated the proportion of that total belonging to different species. The transformation standardized the data for differences in sampling effort. Two of the 13 species sampled effectively by our traps (red-backed voles, *Clethrionomys gapperi*, and deer mice, *Peromyscus maniculatus*) were ubiquitous and common residents in virtually all sites and years of the study. The distributions of their proportions were unimodal and more or less symmetrical. These values were entered as continuous independent variables. Samples of all remaining species were dominated by cases where they were absent from the assembly. The proportion of the assemblage composed of these sparse species was transformed into present vs absent categories, and each species was entered into the analysis as a binary independent variable. The analyses were designed to answer five key questions.

Does the regional community vary from year to year?

Each year of small mammal data is represented by multiple samples (e.g. 8 plots and 4 transects). A high classification success in the MRL analysis would mean that the various samples belonging to a single a priori group (the year data were collected) were more similar to one another than they were to other groups (the remaining years). We would conclude that the relative abundances of species were different each year (temporal stochasticity). A low classification success would mean the opposite. We would be unable to predict which year the samples belonged to because the relative abundances of species, averaged over all samples, were more or less the same each year (evidence for deterministic assembly).

Does community composition within years vary with location?

My data correspond to samples from only forest habitat (plots) as well as those from both forest and cutovers (transects). If different sites possess different temporal patterns, then the classification success should be high because communities in the plots are different than communities in the cutovers (spatial stochasticity, 2 groups of data–plots versus transects [controlled by habitat]).

Are nearby assemblies more similar to one another than to distant ones?

The eight forest plots, and two of the transects, were located in a single conifer stand (the cutover segments of the transects had been harvested). The other two transects were located approximately 5 km away in two different stands (Appendix 1). If different sets of communities (3 groups–plots, nearby transects, distant ones) possess different temporal patterns in species composition, then the classification success of those analyses (controlling for habitat) will again be high (more evidence for spatial stochasticity).

Does community assembly vary with habitat?

Comparisons between plots and transects are confounded by two effects. The transects were located in different sites than were the plots, and they also included cutover habitat. I controlled for the effect of habitat by first comparing plots with only the forest segments of the transects, then repeated the analyses by including data from the cutovers. If community composition varies with habitat, then the classification success should be higher in analyses that include cutovers than in analyses using only forest data (evidence for deterministic assembly based on habitat).

Are the relative abundances of common species less variable than the composition of the overall community?

The roles of spatiotemporal stochasticity should be greatest for sparse species. Thus, the relative abundances of more or less ubiquitous species should be more predictable (low classification success) than is the composition of the overall community of small mammals (evidence for stochasticity of sparse species as well as deterministic assembly creating correlated abundances of common species).

Multinomial logistic regression

I classified the small mammal assemblages using 18 MLR analyses (main effects only, SPSS, version 11, Table 1) comprising different (non-independent) subsets of the assembly data. I began by partitioning the dependent variable (time in this example) to represent different years of the study, and analyzed those data in four different ways. I used two different subsets of the data. In one pair of analyses (numbers 1 and 2 in Table 1), I included assembly data calculated separately for each of the eight plots, plus those corresponding only to the forest segments of the transects (referred to as "forest only"). I analyzed both the complete community, as well as the subassembly composed of the two nearly ubiquitous and common species (*Peromyscus* and *Clethrionomys*). I used the same plot data in a second pair of analyses (numbers 3 and 4 in Table 1), but with transect data accumulated from both forest and cutover segments. Thus, the four different MLR models assessed the annual variability in, respectively, 1) the complete assemblage of small mammals in mature forest habitat only, 2) the subassemblage of voles and mice in forest only, 3) the full assembly in both forest and cutover habitats, and 4) the subassembly of voles and mice in both habitats. Since the plot and transect data represent different temporal sequences, each annual analysis was performed separately on the complete sequence of years using data only from plots (numbers 5 and 6 in Table 1), and on the set of years where data existed for both plots and transects (analysis numbers 1–4).

Table 1. Summary of 18 different multinomial logistic regression analyses on a community of 13 small mammal species living in the boreal forest of northern Ontario, Canada. "Number" refers to the number given to each analysis in the methods section.

Species	Number	Comparison	N	χ^2	P
		Analyses including mature forest only			
13	5	among 12 yr in 8 forest plots	96	473.0	<0.001
Cg and Pm	6		96	156.2	<0.001
13	1	among 6 yr in plots and transects	72	258.0	<0.001
Cg and Pm	2		72	91.8	<0.001
13	7	among 3 groups (plots and transects)	72	44.6	0.006
Cg and Pm	9		72	10.2	0.037
13	11	among 2 groups (plots vs transects)	72	33.7	0.001
Cg and Pm	13		72	8.4	0.015
13	15	among 12 plots and transects	72	238.1	<0.001
Cg and Pm	16		72	26.0	0.25
		Analyses including both forest and cutover habitats			
13	3	among 6 yr with forest and cutover	72	258.0	<0.001
Cg and Pm	4		72	83.2	<0.001
13	8	among 3 groups (plots and transects)	72	124.9	<0.001
Cg and Pm	10		72	38.9	<0.001
13	12	among 2 groups (plots vs transects)	72	91.7	<0.001
Cg and Pm	14		72	31.6	<0.001
13	17	among 12 plots and transects	72	280.6	<0.001
Cg and Pm	18		72	53.0	<0.001

I repeated the analyses to assess the joint effects of space and scale using three additional ways of partitioning the data among a priori "spatial" classifications. Again, each analysis was restricted to only those years where each spatial partition of the data was represented equally through time. First, I partitioned the dependent spatial variable into three groups representing a) the eight forest plots, b) the nearby pair of transects, and c) the two distant transects. I analyzed the data, as above, by evaluating the complete assemblage in mature forest habitat only (number 7 in Table 1), then in both habitats (number 8), then repeated the analyses with the subassemblage of red-backed voles and mice (numbers 9 and 10). I repeated the four analyses using a binary classification (plots vs transects, numbers 11–14 in Table 1), and concluded with four analyses partitioned into 12 classes representing the 12 different sampling sites (numbers 15–18 in Table 1). These analyses allowed me to determine, for example, whether the small mammal assemblages in the forest plots were different from those occurring along near and distant transects (differences in scale, analysis numbers 7–10). The second set of (binary) analyses (numbers 11–14) allowed me to evaluate whether assemblages in the plots were different from those represented by transects (mostly differences among habitats). The final set of analyses (15–18) tested whether the effects of spatial scale occurred at finer levels of resolution.

Interpreting the MRL analyses

Interpretation of the results is confounded because the MRL analyses do not represent independent partitions of the variance in mammal assemblies. Thus, rather than interpreting each analysis separately, I compare the classification success of the different analyses to gain insights into the roles of time, space, scale, and habitat on community composition. If, for example, the composition of the small mammal assemblage on each plot and transect changes the same way each year, most plots and transects included in the analyses (1–6) of annual differences should be classified properly in time (high classification success). If the patterns from the two dominant species are redundant with those of the rest of the assemblage, the classification success of analyses restricted to these species (analysis numbers 2, 4, and 6) will be similar to those obtained from the overall assembly (1, 3, and 5).

I assessed the importance of spatial variation similarly. If the assemblies along transects are more similar to one another than they are to the assemblies in the plots, the classification success of the analyses contrasting the four transects vs plots will be high (numbers 11–14, Table 1). Recall, in these analyses, that the groups represent my a priori categories for comparison, the samples themselves are not pooled (all sample sizes were ≥ 72). A high classification success would mean that most of the separate samples were correctly assigned to either the group of 8 plots, or to the group of 4 transects. A high classification success would remain when the transects are further subdivided into two groups (analysis numbers 7–10) if the assemblages within the large jack pine–spruce stand are different from those in the more distant stands. But a low classification success would emerge in the comparison of all 12 plots and transects (analysis numbers 15–18) if the same assemblage is found in different plots or transects.

Why use MLR? Why not calculate a similarity matrix, cluster the data, and search for patterns? The reason is simple. A similarity matrix excludes information on species identity. I am interested in more than the correlation structure of the samples. I want to assess, explicitly, how different a priori temporal and spatial slices of the data reveal the relative roles of time, space, scale, and habitat on the overall assembly.

Sampling from species–abundance distributions

Let's be clear on the analysis and its assumptions. The species–abundance distribution of small mammals, like that of virtually all communities, has a few very abundant species and many rare ones. Imagine, for the sake of argument, that the actual species–abundance distribution in a region is fixed. If one draws a small number of random samples from such a community (e.g. one each year), most will be unique. My analyses (numbers 1, 3 and 5 in this example) would achieve a high classification rate by chance alone, and would reveal little about correlated abundances. If the rare species were eliminated from the analysis, communities would be much more similar, and the classification rate would decline (numbers 2, 4, and 6). Again, I would learn little, if anything, about processes structuring communities. The same results would apply if random samples were drawn in different areas.

But now imagine that the (annual) samples themselves are comprised of numerous subsamples (as collected in different plots and transects). If the species–abundance distribution is fixed, each of the subsamples will be more or less unique. The central limit theorem dictates that the "mean assemblages" accumulated across subsamples for each different year will all fit the same distribution because every subsample is drawn separately from the (same) overall species–abundance distribution. All of the years will possess a similar assemblage of species and the classification rate according to year will be small.

Finally, imagine that species abundances vary in response to local and regional processes, or simply reflect larger scale influences (e.g. neutral communities (Hubbell 2001), regional similarity (Mouquet and Loreau 2002), or locations in geographical ranges (McGill and Collins 2003)). Below some set of scales in space and time, the species–abundance distribution would be similar for all subsamples. If those subsamples adequately represent the community at that scale, they too will be similar, and will be classified together (low success). But if the community varies at even lower levels of resolution, each subsample will be unique, and the classification success would be high at that scale.

Thus, in my analyses, if species abundances vary predictably through small scales in space and time (e.g. samples from separate plots and transects), the classification success at that low level of resolution will be high. If species abundances vary at larger scales, the classification success at those higher levels will be high.

A related caveat concerns my separate analyses of the entire assemblage vs that of the two dominant species (*Clethrionomys* and *Peromyscus*). Should we not expect the sub-assembly of only two common species to be more homogeneous than that of the entire assemblage that includes many sparse species? The answer is yes, if we analyze both groups at the same scale of resolution. But I did not. I used presence–absence data for sparse species, and proportional abundances for red-backed voles and deer mice. I thus required a higher level of consistency in assembly structure when I examined the spatio-temporal and habitat patterns for only voles and mice, than I did in my analyses of the entire assemblage. The vole–mouse subassembly would yield a lower classification success than the entire assembly only if the fine scale relative abundances of those two species through time, space, and habitat are more homogeneous than the course scale presence and absence of the other species.

Results

Our samples, comprising a total of 13 710 small mammal captures, revealed a dynamic and diverse mix of 13 species with a typical "log-normal" species–abundance distribution (illustrated for the eight plots in Fig. 2). The small mammal assembly represented six different guilds. The largest guild was composed of predominantly herbivorous microtine rodents (*Clethrionomys gapperi*, *Microtus chrotorrhinus*, *M. pennsylvanicus*, *Phenacomys intermedius* and *Synaptomys cooperi*). Other rodent guilds included the two diurnal sciurids (*Tamias minimus*, *T. striatus*), the two zapodids (*Napaeozapus insignis*, *Zapus hudsonius*), and the single cricetid (*Peromyscus maniculatus*). The shrews represented two additional insectivore guilds comprised of the single large *Blarina brevicauda*, and the two similar-sized *Sorex* (*S. arcticus*, *S. cinereus*) (Fox and Kirkland 1992).

Though sampling effort varied among years, it is noteworthy that the composition of combined small mammal assemblies among plots, or separately among transects, were unique in each and every year (Appendix, Table A1 and A2). We can thus anticipate (at least for the analyses including all 13 species) significant logistic regressions with high classification rates. Unique combinations of species were also often found on different plots (or transects) through time (below).

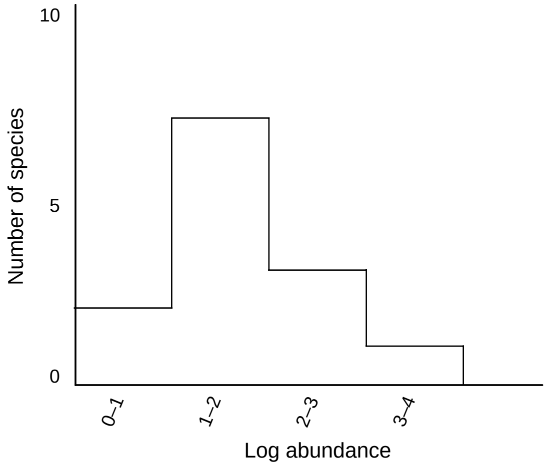

Fig. 2. The cumulative species–abundance (number of individuals) distribution of 13 small mammal species captured over a period of 12 years on eight 1 ha study plots in the boreal forest of northern Ontario, Canada. The rank order of species abundances is as follows: Class 1 – *Sorex arcticus*, *Tamias minimus*; Class 2 – *Blarina brevicauda*, *Microtus pennsylvanicus*, *Napaeozapus insignis*, *Phenacomys intermedius*, *Synaptomys cooperi*, *Tamias striatus*, *Zapus hudsonius*; Class 3 – *M. chrotorrhinus*, *Peromyscus maniculatus*, *Sorex cinereus*; Class 4 – *Clethrionomys gapperi*.

The vast majority of multinomial logistic regressions were indeed highly significant (15 out of 18 analyses) and yielded an almost perfect classification of samples (Table 1, Fig. 3). Contrasts including all 13 species produced higher classifications than did contrasts with only voles and mice, but often, only a subset of species contributed significantly to the final logit model. My purpose, however, was to evaluate the patterns in classification, not the best models including the fewest species. Thus, I retained all independent variables when interpreting the following classification patterns.

When data for all 13 species were contrasted in forest habitat, only a single year was misclassified (and only for some plots, Fig. 3). When the data including both habitats were contrasted, each year and each spatial grouping (2 groups: plots plus near transects vs distant transects, 3 groups: plots vs near transects vs distant transects) was unique (100% of the samples were classified correctly). Even when the spatial comparisons

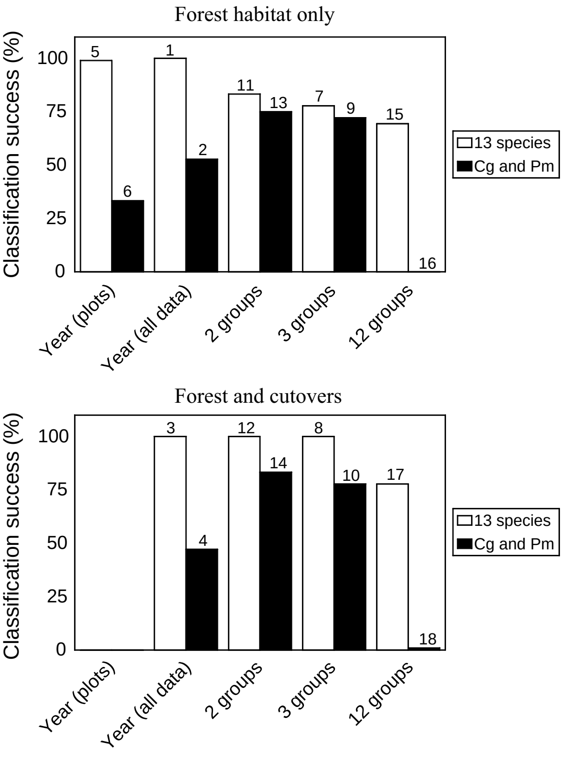

Fig. 3. The classification success (% of samples classified correctly) of 18 different multinomial logistic regressions assessing differences in small mammal communities through time (years), space (different groupings of plots and transects), and habitat (forest only vs forest plus cutover data). Separate analyses were conducted on the entire set of species in the community ("13 Species") as well as on only the relative abundances of red-backed voles and deer mice ("Cg and Pm"). The first pair of analyses in the lower panel is absent because the plots included only forest habitat. Numbers above each bar correspond to the analysis numbers given in Table 1.

were broken into 12 different groups (8 plots, 4 transects), more than three quarters of the 72 samples were classified to their proper spatial group (Table 1, Fig. 3). When only data from the mature forest stands were compared, the temporal classification was unaltered, but the classification success by spatial groupings declined (Fig. 3).

The results differed dramatically when only data on the relative abundances of *Clethrionomys* and *Peromyscus* were used in the analyses. Spatial classifications including grouped plots retained a highly unique signature (high classification success). But temporal analyses, as well as those that contrasted all of the plots and transects individually, revealed large redundancies in composition (all classifications approximately 50% or less). The classification success was lowest, by far, when all plots and transects were treated individually. As with the analysis of all 13 species, more samples tended to be classified correctly in comparisons that included both habitats than for comparisons within the forest habitat alone.

Similarly, individual samples collected on a single plot or transect are redundant with other samples within a given year (they all classify together). But as the small mammal assembly changes through time, groups of nearby samples tend to vary together. This complex pattern of spatial–temporal correlation can be interpreted as follows:

1) When I searched for differences in the ‘regional’ small mammal assembly among years (“year” in Fig. 3), the spatial variance among plots and transects in any one year was small compared to the year-to-year variance.
2) When I searched, instead, for differences among locations (e.g. plots vs transects, “2 groups” in Fig. 3), the annual variance within nearby samples was less than the spatial variance among more distant groups of samples.
3) But when I attempted to classify individual plots or transects with data from different years (“12 groups” in Fig. 3), the temporal variance within plots was swamped by the combined spatial-temporal variance in the assembly.
4) Even so, different habitats tended to support different assemblies of species (“forest” vs “forests and cutovers” in Fig. 3).
5) And the relative abundances of the two common species were less variable than was species composition.

Thus the small mammal assembly, as a whole, defies description as the sets of samples for each comparison represent unique combinations of species and their relative abundances. But, when the two dominant species only are compared, the separate “community” samples are far more redundant. The joint population dynamics of the two species are similar among near neighbourhoods in space, as well as through time.

Does this mean that the structure of communities, at these scales, is determined only by stochastic processes? I attempted to answer this question by evaluating whether the assemblies obey Fox’s rule: “species entering a community will tend to represent different guilds until all guilds are present, before the rule repeats” (Fox 1987, Fox and Brown 1993, Morris and Knight 1996).

I assumed, as in an earlier analysis with Tom Knight (Morris and Knight 1996), that all species had an equal opportunity, at the mesoscale of this study, to occupy any assembly (I address this assumption in Appendix 2). I then used the accumulated data (Appendix 2) on plots and transects (23 samples) to evaluate whether the overall assemblies obey Fox’s rule (some prefer to call this a pattern, Belyea and Lancaster 1999). Thus, my analysis for agreement with the rule corresponds to the same scale as my main analyses of variation in assemblies through time (12 years) and space (2 groups). The theory should apply to the entire set of six different guilds that yields 647 different combinations of species (648 if we include the “no mammals present” assembly). But with only 23 samples, I restricted my analyses to the less diverse rodent assemblies (107 possible combinations).

The 23 samples are represented by 10 “non-Fox” and 13 “Fox” assemblies (Appendix 2). The ratio departs dramatically from the approximately 25% (26/107) of all possible states that represent Fox assemblies. I calculated the expected number of assemblies obeying Fox’s rule by first calculating the frequencies of assemblies composed of differing numbers of species (Morris and Knight 1996). For each of those frequencies, I counted the number of expected Fox assemblies, then calculated the total expected in my data. There are, for example, 18 different possible 5 species assemblies. Two of these obey Fox’s rule. Six of the 23 samples were composed of five species. Thus, the expected number of assemblies obeying Fox’s rule is given by $([2/18]6) = 0.67$. I repeated similar calculations for assemblies of all sizes (up to 10 rodent species) to generate the overall expected number of Fox states (3.36) in these data. I converted the expected number of Fox assemblies into the expected proportion overall, then calculated the cumulative binomial probability of observing 13 or more Fox assemblies. The analysis reconfirms our earlier research (Morris and Knight 1996). Fox assemblies, even when accumulated through time and aggregated through space, were much more frequently observed than expected by chance alone ($P \ll 0.001$, see Appendix 2 for a more conservative, but still highly significant, test result).

Stochastic effects in community assembly are linked to species differences in life history, abundance, and potential for movement. My MRL analyses addressed the issue of abundance explicitly, but not differences in basic life history. Four of the species (zapodids and sciurids) hibernate. Assuming that predation rates are similar for mammals of similar size, hibernation should reduce annual variation in predator-induced mortality. Hibernating species should be more predictable members of assemblies than nonhibernating species. My data are equivocal on this point. Hibernating least chipmunks occupied all transects, but so too did nonhibernating deer mice (Table A2). Hibernating *Zapus* and *Napaeozapus* were usually present in the forest plots, but had somewhat different occurrences on the transects (compare Table A2 with Table A1).

Species differences among functional groups will not influence Fox's rule, but differences among species within groups might. Potential to occupy a local assembly could, for example, be greater for vagile species than for more sedentary ones. I attempted to assess this issue by calculating the maximum inter-capture distance of rodents occurring on transects (I have too few repeat captures on shrews to include them in the analysis). I maximized sample sizes by including data from our earlier study (Morris and Knight 1996) that used identical 390 m long transects. I included only those individuals that were captured two or more times and excluded any individual captured in the most distal stations (0 and 390 m) along a transect. I searched for species differences with a univariate analysis of variance on maximum inter-capture distance with species as a fixed factor, and with numbers of captures as a covariate.

Inter-capture distance increased with the number of captures recorded ($F_{1,733} = 74.9$, $P < 0.001$), but the covariate did not obscure clear differences among species ($F_{8,733} = 13.0$, $P < 0.001$). The two sciurids were more vagile than the other species in the community (Fig. 4). *Zapus* and *Peromyscus* appeared to possess larger inter-capture distances than other rodents of similar size. It is thus possible that the two zapodid species would tend to generate more assemblies with only *Zapus*, than with both species present (but see Appendix 2). A similar "bias" does not apply to the two sciurids.

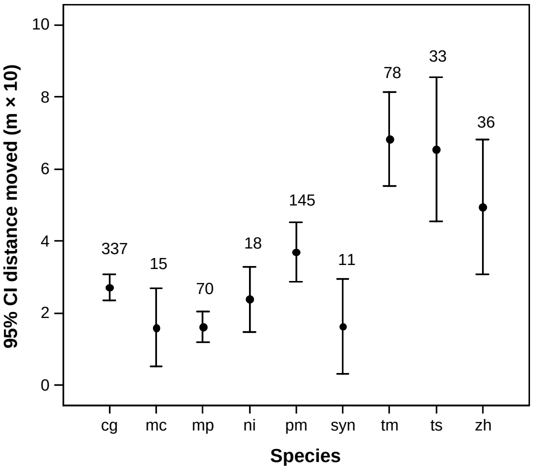

Fig. 4. Means and confidence intervals of the maximum distance between capture points for rodents living along 19 different 390 m long transects in northern Ontario, Canada. The data include only animals captured two or more times, and exclude all animals that were captured at the most distal stations of a transect (0 and 390 m, numbers correspond to sample sizes). Short forms as follows: cg – *Clethrionomys gapperi*, mc – *Microtus chrotorrhinus*, mp – *Microtus pennsylvanicus*, ni – *Napaeozapus insignis*, pm – *Peromyscus maniculatus*, syn – *Synaptomys cooperi*, tm – *Tamias minimus*, ts – *Tamias striatus*, zh – *Zapus hudsonius*.

Discussion

Boreal rodent assemblages living in upland conifer stands in northern Ontario represent a highly-diverse but largely ephemeral and apparently serendipitous collection of core and satellite species (Hanski 1982). Individually, sparse species appear and disappear from study areas with no clear temporal or spatial pattern. But collectively, the overall assembly is similar at the same time in different places, and is similar in the same general area at different times. Species do not enter and leave an assemblage in a completely haphazard manner. Instead, they obey predictable probabilistic rules of assembly. When the microtine guild is diverse, for example, so too are the other guilds. When one guild has few members, other guilds tend to follow suit. The apparent paradox between random and predictable assembly emerges from asynchronous scales in space and time, and by the way we examine communities. If we look for differences in samples of communities collected at different times, we will find them (Fig. 1). And, if we look for differences in community samples collected in different places, we will find those also. But if we expand our view to search for repeated patterns involving the entire community, our focus on differences in species occurrence disappears into a mosaic background of predictable assemblies.

Spatial and temporal variability also tends to disappear when we restrict our attention to the two co-dominant core species (*Clethrionomys* and *Peromyscus*). The actual and relative abundances of red-backed voles and deer mice were similar in different years (poor annual classifications), and among nearby sample plots (even poorer classification among the 12 different spatial samples). But populations of the two species living in different locations tended to possess different patterns in their dynamics (e.g. high classification success when I contrasted one group representing plots with another one representing transects).

The pattern would thereby appear most consistent with metapopulation models of core and satellite species where rescue effects and species differences in colonization and extinction generate either widespread ubiquitous species, or narrowly distributed sparse species (Hanski 1982, 1999, Hanski and Gyllenberg 1993, but see Nee et al. 1991). There are at least three reasons to be suspicious about the metapopulation "conclusion". 1) Core and satellite patterns can emerge from niche differences between abundant and widespread generalists, versus sparse and narrowly distributed specialists (Brown 1984, 1995). The generalist–specialist interpretation is attractive because niche-based models also yield Fox's rule (Morris and Knight 1996). 2) The spatial scale of my study (and most especially that of the forest plots) is likely too small to invoke exctinction and colonization explanations for species distribution (Appendix 2). 3) The most vagile species in the assembly (and thus, presumably, the best colonizers) are not the most widely distributed.

Thus a more balanced interpretation is that the abundances and distributions of red-backed voles and deer mice are regulated by strong and predictable interactions (driven, perhaps, by predation rather than competition, Morris 1996), while the dynamics of the other species reflect weak interactions and poorly understood or random processes of invasion and persistence. The overall assemblage would thereby reflect a compromise between strong and deterministic influences operating on the two abundant and permanent rodents, but with a predominant random assembly for the majority of species. I am uncertain whether such a compromise would be acceptable by either side in the neutral versus deterministic debate on community assembly.

Supporters of a deterministic perspective would properly note that my sampling and analyses only partially include the effects of habitat that are known to play key roles in the coexistence and assembly of northern small mammal species (Morris 1983, 1984, 1996, Vickery et al. 1989, Morris and Knight 1996). Cutover habitats, for example, typically include different members of rodent guilds (e.g. *Zapus* versus *Napaeozapus*, *M. pennsylvanicus* versus *M. chrotorrhinus*) than do adjacent forests (Morris and Knight 1996). It is likely, therefore, that our long term data on boreal small mammals overestimates the importance of "random" assembly. Our method of sampling also over-estimates the influence of chance assembly. Populations of all species increase during the summer reproductive season, and our chances of detecting sparse species would thereby be reduced for those samples when we did not trap in late summer (e.g. 1999, 2001).

Proponents of the various unified theories of macroecology (Brown 1995, Maurer 1999, Hubbell 2001, Mouquet and Loreau 2002, 2003, McGill and Collins 2003) could counter by noting that insufficient sampling cannot explain "eruptions", and subsequent disappearances, of species. Bog lemmings (*Synaptomys cooperi*) were absent from most of our samples, but were captured on most grids and transects in 2001. Rock voles (*Microtus chrotorrhinus*) were abundant in 1992 and 1994 (100 and 65 animals respectively), but have been sporadic ever since. *Sorex cinereus* was common in 1994 (58 animals), 2000 (120), and 2003 (48), whereas another shrew, *Blarina brevicauda*, was common in 1999 (52 animals), despite our limited sampling, and has been virtually absent ever since (1 shrew on plot 11 in 2003).

Skeptics concerned about the choice of "null" models might argue that my inference about the apparently strong interaction between *Clethrionomys* and *Peromyscus* is an artefact of sampling. "Random" draws of common species will contain more structure than will draws of sparse species. Recall that I reduced this effect by demanding even more structure for common species because they were represented by proportional abundances whereas the data on sparse species included only presence and absence. But even if my results were an "artefact" caused by comparisons among sparse and common species, so what? Why are some species consistently common, while others are not? Why are the common species' relative abundances so consistent? The skeptics who favor purely "neutral process" would win their day in court only if they could, 1), account for the underlying species–abundance distribution, 2), explain the correlated relative abundances of the common species through time and space, and 3) demonstrate that these patterns are exclusive of strong interactions at larger scales in space and time. My opinion on the matter is clear. Readers can judge for themselves whether the burden of proof represented by the repeated and covarying dynamics of voles and mice are more reflective of neutral or deterministic assembly.

How do we reconcile the two divergent, and so inexplicably intransigent, schools of thought? When species such as rock voles and bog lemmings are absent from the assembly, they reduce the number of species within the "vole" guild. But the absence of some species has little effect on the underlying habitat-dependent processes that determine guild membership in the assembly. The rules of local assembly are not broken just because some species enter and leave the community. Yet it is equally apparent that the invasion and persistence of many species are determined, at larger scales, by poorly understood processes. I suspect, if we had sufficient data on regional abundance and distribution, that processes such as dispersal-driven metapopulation and source–sink dynamics would explain some, but not all, of the variation in our local assemblies. Thus, membership in the species pool available to occupy our study plots is shaped, at our scales of resolution, by stochastic processes of species invasion and persistence. But the probabilities that those species will form repeated assemblies are determined by the predictable consequences of sharing resources and predators in variable habitats. At the level of interacting species we do not know whether their dynamics are chaotic, whether the assemblage has one or many stable states interrupted by stochastic influences, whether its trajectory is following a strange attractor, or whether the variability in species abundances is contingent on the history of previous interactions and assembly. It may not even make sense to think about, let alone test for, these various alternatives with boreal small mammals. Even if we could reveal the underlying consumer–resource mechanisms that apply to each species, we would often be unable to predict the exact composition of the community because the assembly mechanics operate at the level of guilds (Samuels and Drake 1997). We can be certain for this group of boreal mammal species, however, that the emergent local assemblage is not random, completely driven by dispersal, or purely predictable. Community membership is open but depends on both locally deterministic and "neutral" rules of assembly.

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References

Bellwood, D. R., Wainwright, P. C., Fulton, C. J. et al. 2002. Assembly rules and functional groups at global biogeographical scales. – Funct. Ecol. 16: 557–562.

Belyea, L. R. and Lancaster, J. 1999. Assembly rules within a contingent ecology. – Oikos 86: 402–416.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. – Am. Nat. 124: 255–279.

Brown, J. H. 1995. Macroecology. – Univ. of Chicago Press.

Brown, J. H., Fox, B. J. and Kelt, D. A. 2000. Assembly rules: desert rodent communities are structured at scales from local to continental. – Am. Nat. 156: 314–321.

Brown, J. H., Kelt, D. A. and Fox, B. J. 2002. Assembly rules and competition in desert rodents. – Am. Nat. 160: 815–818.

Chase, J. M. 2003. Community assembly: when should history matter? – Oecologia 136: 489–498.

Drake, J. A. 1990. The mechanics of community assembly and succession. – J. Theor. Biol. 147: 213–234.

Drake, J. A. 1991. Community-assembly mechanics and the structure of an experimental species ensemble. – Am. Nat. 137: 1–26.

Drake, J. A., Flum, T. E., Witteman, G. T. et al. 1993. The construction and assembly of an ecological landscape. – J. Anim. Ecol. 62: 117–130.

Drake, J. A., Huxel, G. R. and Hewitt, C. L. 1996. Microcosms as models for generating and testing community theory. – Ecology 77: 670–677.

Drake, J. A., Zimmerman, C. R., Purucker, T. et al. 1999. On the nature of the assembly trajectory. – In: Weiher, E. and Keddy, P. (eds), Ecological assembly rules: perspectives, advances, retreats. Cambridge Univ. Press, pp. 233–250.

Eccard, J. A. and Ylönen, H. 2003. Interspecific competition in small rodents: from populations to individuals. – Evol. Ecol. 17: 423–440.

Fargione, J., Brown, C. S. and Tilman, D. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. – Proc. Natl. Acad. Sci. (USA) 100: 8916–8920.

Fox, B. J. 1987. Species assembly and the evolution of community structure. – Evol. Ecol. 1: 201–213.

Fox, B. J. 1999. The genesis and development of guild assembly rules. – In: Weiher, E. and Keddy, P. (eds), Ecological assembly rules: perspectives, advances, retreats. Cambridge Univ. Press, pp. 23–57.

Fox, B. J. and Brown, J. H. 1993. Assembly rules for functional groups in North American desert rodent communities. – Oikos 67: 358–370.

Fox, B. J. and Kirkland, G. L. 1992. An assembly rule for functional groups applied to North American soricid communities. – J. Mammal. 73: 491–503.

Fryxell, J. M., Falls, B., Falls, E. A. et al. 1998. Long term dynamics of small mammal populations in Ontario. – Ecology 79: 213–225.

Gaston, K. J. and Blackburn, T. M. 2001. Macroecology. – Blackwell Science.

Gillespie, R. 2004. Community assembly through adaptive radiation in Hawaiian spiders. – Science 303: 356–359.

Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. – Oikos 38: 210–221.

Hanski, I. 1999. Metapopulation ecology. – Oxford Univ. Press.

Hanski, I. and Gyllenberg, Y. 1993. Two general metapopulation models and the core-satellite species hypothesis. – Am. Nat. 142: 17–41.

Henttonen, H., McGuire, A. D. and Hansson, L. 1985. Comparisons of amplitudes and frequencies (spectral analyses) of density variations in long term data sets of *Clethrionomys* species. – Ann. Zool. Fenn. 22: 221–227.

Holt, R. D. 1993. Ecology at the mesoscale: the influence of regional processes on local communities. – In: Ricklefs, R. E. and Schluter, D. (eds), Species diversity in ecological communities: historical and geographical perspectives. Univ. of Chicago Press, pp. 77–88.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. – Princeton Univ. Press.

Kotler, B. P. and Brown, J. S. 1999. Mechanisms of coexistence of optimal foragers as determinants of the local abundance and distributions of desert granivores. – J. Mammal. 80: 361–374.

Krebs, C. J., Boutin, S. and Boonstra, R. (eds) 2001. Ecosystem dynamics of the boreal forest: the Kluane project. – Oxford Univ. Press.

Krebs, C. J., Kenney, A. J., Gilbert, S. et al. 2002. Synchrony in lemming and vole populations in the Canadian Arctic. – Can. J. Zool. 80: 1323–1333.

Law, R. and Morton, R. D. 1993. Alternative permanent states of ecological communities. – Ecology 74: 1347–1361.

Lawler, S. P. 1993. Direct and indirect effects in microcosm communities of protists. – Oecologia 93: 184–190.

Lockwood, J. L., Powell, R. D., Nott, M. P. et al. 1997. Assembling ecological communities in time and space. – Oikos 80: 549–553.

Luh, H.-K. and Pimm, S. L. 1993. The assembly of ecological communities: a minimalist approach. – J. Anim. Ecol. 62: 749–765.
Lundberg, P., Ranta, E., Ripa, J. et al. 2000. Population variability in space and time. – Trends Ecol. Evol. 15: 460–464.
MacArthur, R. A. 1972. Geographical ecology. – Harper and Row.
Marcström, V., Höglund, N. and Krebs, C. J. 1990. Periodic fluctuations in small mammals at Boda, Sweden from 1961 to 1988. – J. Anim. Ecol. 59: 753–761.
Maurer, B. A. 1999. Untangling ecological complexity. – Univ. of Chicago Press.
McGill, B. 2003. A test of the unified neutral theory. – Nature 422: 881–885.
McGill, B. and Collins, C. 2003. A unified theory for macroecology based on spatial patterns of abundance. – Evol. Ecol. Res. 5: 469–492.
Mora, C., Chittaro, P. M., Sale, P. F. et al. 2003. Patterns and processes in reef fish diversity. – Nature 421: 933–936.
Morris, D. W. 1983. Field tests of competitive interference for space among temperate-zone rodents. – Can. J. Zool. 61: 1217–1223.
Morris, D. W. 1984. Patterns and scale of habitat use in two temperate-zone small mammal faunas. – Can. J. Zool. 62: 1540–1547.
Morris, D. W. 1996. Coexistence of specialist and generalist rodents via habitat selection. – Ecology 77: 2352–2364.
Morris, D. W. and Knight, T. W. 1996. Can consumer–resource dynamics explain patterns of guild assembly? – Am. Nat. 147: 558–575.
Morton, R. D., Law, R., Pimm, S. L. et al. 1996. On models for assembling ecological communities. – Oikos 75: 493–499.
Mouquet, N. and Loreau, M. 2002. Coexistence in metacommunities: the regional similarity hypothesis. – Am. Nat. 159: 420–426.
Mouquet, N. and Loreau, M. 2003. Community patterns in source–sink metacommunities. – Am. Nat. 162: 544–557.
Nee, S. and Stone, G. 2003. The end of the beginning for neutral theory. – Trends Ecol. Evol. 18: 433–434.
Nee, S., Gregory, R. D. and May, R. M. 1991. Core and satellite species: theory and artefacts. – Oikos 62: 83–87.
Norušis, M. J. 1999. SPSS Regression Models 10.0. – SPSS Inc., Chicago.
Oksanen, L. and Oksanen, T. 1992. Long term microtine dynamics in north Fennoscandian tundra: the vole cycle and the lemming chaos. – Ecography 15: 226–236.
Pimm, S. L. 1991. The balance of nature?. – Chicago Univ. Press.
Post, W. M. and Pimm, S. L. 1983. Community assembly and food web stability. – Math. Biosci. 64: 169–192.
Ranta, E., Kaitala, V. and Lindström, J. 1999. Spatially autocorrelated disturbances and patterns in population synchrony. – Proc. R. Soc. Lond. B, 266: 1851–1856.
Ricklefs, R. and Schluter, D. (eds) 1993. Species diversity in ecological communities: historical and geographical perspectives. – Univ. of Chicago Press.
Samuels, C. L. and Drake, J. A. 1997. Divergent perspectives on community convergence. – Trends Ecol. Evol. 12: 427–432.
Stone, L., Dayan, T. and Simberloff, D. 2000. On desert rodents, favored states, and unresolved issues: scaling up and down regional assemblages and local communities. – Am. Nat. 156: 322–328.
Tilman, D. 1982. Resource competition and community structure. – Princeton Univ. Press.
Vickery, W. L., Iverson, S. L., Mihok, S. et al. 1989. Environmental variation and habitat separation among small mammals. – Can. J. Zool. 67: 8–13.
Weiher, E. and Keddy, P. (eds) 1999a. Ecological assembly rules: perspectives, advances, retreats. – Cambridge Univ. Press.
Weiher, E. and Keddy, P. 1999b. Assembly rules as general constraints on community composition. – In: Weiher, E. and Keddy, P. (eds), Ecological assembly rules: perspectives, advances, retreats. Cambridge Univ. Press, pp. 251–271.
Wilson, D. S. 1992. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. – Ecology 73: 1984–2000.
Ylönen, H. and Kotler, B. P. 2003. Costs of coexistence in mammals. – Evol. Ecol. 17: 313–314.
Ziv, Y. and Kotler, B. P. 2003. Giving-up densities of foraging gerbils: the effect of interspecfic competition on patch use. – Evol. Ecol. 17: 333–347.

Appendix 1

Description of study sites and field methods

The eight forest plots were placed in a single large (~500 ha) fire-origin forest stand dominated by 80-yr-old jack pine and black spruce. The forest floor consists mostly of a vibrant green carpet of feathermosses (notably *Pleurozium shreberi*, *Ptilium crista-castrensis* and *Hylacomium splendens*), with an understorey composed of shrubs such as alder (*Alnus viridis*), honeysuckle (*Diervilla lonicera*), and blueberries (*Vaccinium angustifolium*, *V. myrtilloides*). Dominant herbs include bunchberry (*Cornus canadensis*), gaywings (*Polygala paucifolia*), and goldthread (*Coptis trifolia*).

The four census transects bisected conifer stands and adjacent (approximately) 15-yr-old cutovers. Two transects were located within the same jack pine–spruce stand as were the eight permanent plots (but approximately 200 m from the nearest plot, these are referred to as "near" transects). The other two ("distant" transects) were located 5 km away in similar aged fire-origin-pine-dominated stands. One half of each transect extended into the native forest, the other 20 stations reached into the adjacent cutover. Three cutovers were dominated by 5 m tall jack pine, the fourth had been planted to black spruce. Though two cutovers (one pine, one spruce) were used by foresters in family tests for tree improvement studies, tree and shrub (mainly *Alnus viridus*) densities and sizes were similar in all transects dominated by regenerating jack pine. The spruce testplot, reflecting tree growth form, had less overhead vegetation, and a more exposed forest floor, than the others. Mats of feathermoss had not yet re-established in cutovers that typically had much more grass cover (especially *Calamagrostis canadensis*) than the mature forest stands.

The eight permanent study plots were arranged in a grid of four rows and two columns. Each 100 × 100 m plot was isolated from its nearest neighbour by an intervening "control" plot of equal area. Controls were avoided during the entire study. The outside margin of the "checkerboard" was at least 200 m from any disturbed habitat.

The general area has witnessed extensive forest harvest over the past decade. Regardless, we have maintained approximately 200 contiguous ha of the original stand for our plots and near transects, and slightly less for the distant transects. Normal tree senescence, coupled with extreme wind storms, have produced some local blowdown (usually <10 trees) on study plots as well as occasional crown openings caused by the death of individual trees. There has, however, been no dramatic change in forest composition over the duration of this study.

Single Longworth live-traps baited with a peanut-butter-flour mixture, potato, and mattress stuffing, and covered with an aluminum shelter, were set at each of the 6 × 6 lattice of trap stations (20 m spacing) on a plot, and at each station along transects (10 m spacing). Traps were set in the late afternoon and early evening on day 1 (usually Monday), and were checked at first light and dusk until dawn on day 3 (usually Thursday). Trapping was extended for an additional day on rare occasions when black bears (*Ursus americanus*) destroyed or otherwise vandalized sequences of traps. Live-trapped small mammals were identified to species, marked individually, weighed, measured (body length, tail length), and released at the point of capture. Traps containing animals were replaced with clean ones, and all dirty traps were washed in detergent, sanitized (beginning in 1995), and thoroughly rinsed before being reset. Rodents were living under completely natural conditions except for 1992 and 1993 when six plots received supplemental food as part of a planned experiment.

Each census interval lasted two weeks. Plots 1–4 were trapped in week 1, and plots 5–8 in week two. Pairs of transects were typically trapped either at the same time, or during separate intervals dedicated specifically to transect trapping. The number of census intervals varied among years (Table A3) as various other projects competed for time and resources. The data include complete censusses of all eight plots. Transects were trapped less intensively. On occasion, one or more transects were not censussed early in the study, but all have been trapped during the six-year interval from 1997 through 2003 (only these latter six-years are analyzed here). We attempted to trap both early and late during the summer reproductive season. Census intervals were categorized by the number of weeks elapsed since the normal beginning of trapping that followed snow-melt by mid-May.

Appendix 2

Is equal opportunity the appropriate null model for species assembly?

Using history as a guide (see Brown et al. 2000 and Stone et al. 2000 for a suitably unflattering introduction), ecologists are even less likely to agree on the choice of appropriate null models for community assembly than they are to agree on the relative roles of stochastic vs deterministic processes. I have no interest in re-opening the wounds of those debates, nor do I have any aspiration to change the (apparently) fixed views of the antagonists. Rather I wish to assess, objectively, how best to estimate (and to test for) the expected number of rodent assemblies obeying Fox's rule. Two questions are of pre-eminent importance. 1) Can we assume that all of the rodent species, regardless of their abundance and frequency of occurrence, have equal access to any local assembly? 2) Can we assume that the sampling of sparse species has been adequate to confirm their absence from local assemblies?

Dealing with the first question, imagine a community sampled at several sites that contains two types of species. One type is both abundant and widely distributed, the other is sparse and narrowly distributed. Now, imagine that we collect all of the individuals representing each species, as we would a deck of cards, shuffle them randomly, then deal them back to the sites (controlling for the original number of individuals). Will all sites contain both types? No. Most sites will contain the abundant species. Many sites will contain only one or a few sparse species, and some will contain more. Sites with many individuals will be more likely to contain multiple guilds, and will also be more likely to contain multiple species belonging to a single guild. So it is quite clear that Fox assemblies could emerge from a simple random process. But Fox's rule would emerge only if the occurrence of Fox assemblies greatly exceeds the number generated by chance.

Some ecologists (including a referee of an earlier version of this contribution) may wish to insert even more structure in the null assemblies. Despite the relatively small scale of my sampling, some species may not have equal access to all sites. To consider only one of many possibilities, we might argue that stochastic influences on sparse species could cause their local extinction in a particular year, and thereby exclude them from any assembly at that time. We need a separate deck of cards for each site and year. We shuffle the cards separately for each deck, but deal them all back to the same hand. Voila! With zero degrees of freedom we obtain a perfect correspondence between observed and expected distributions. Fox assemblies are no more common than expected by chance. And so too is our knowledge of any rules of assembly.

Fox's rule emerges not from the relative abundances of individuals in a local assemblage, but from the frequency with which species occur in different assemblies. Using our playing-card example, cards dealt to a hand will tend to belong to different suits until all suits are present before the rule repeats. How could we determine whether any single dealing of the cards obeys the rule? One method would control for the observed frequency of each suit amongst the hands dealt. In this case, each card in a hand represents a different species rather than a different individual; suits correspond to different guilds. Knowing the frequency of each species, we can calculate the exact probability that its suit will occur alone, as a pair, triplet, and so on. Applying this process to boreal rodents in northern Ontario, Fox assemblies were no more common than expected (plots–expected $=0.425$, observed $=0.5$; transects–expected $=0.704$, observed $=0.64$).

But tests of Fox's rule that include the frequency with which different species exist in observed communities are too conservative. In Fox assemblies, species are excluded from "unfavored" states (Fox 1987) by competition (Morris and Knight 1996). When we include the frequency of species in our test, we include the very mechanism of competition that the rule is designed to reveal.

Let's consider a different approach that corresponds to my tests for Fox assemblies. Instead of each individual being represented by its own card, imagine that the number of cards for each species corresponds to the number of sites that it occurs in. Pretend that we shuffle this much smaller deck, and deal one card to each site for every species known to occur there (equal opportunity of occurrence). We will generate the same expected distribution of species in random assemblies from this small deck, as we did from the large one, if frequency of species occurrence at different sites is perfectly correlated with overall abundance. The expected assemblies generated from the two decks will differ from one another if individuals are not distributed at random. The test for Fox assemblies using the small deck will be more robust because it allows for both independent and non-independent assortment of individuals.

Some readers (including a different referee) might think that habitat preferences of guild members (usually interpreted to represent competitive interactions), and numerous sparse species, will tend to generate assemblies with no more than a single species in each guild. And the presence/absence of ubiquitous species comprising a single guild (deer mice) can never be used to differentiate Fox from non-Fox assemblies. A similar criticism could be made about comparisons involving guild members with different home-range sizes (e.g. *Zapus* vs *Napaeozapus*). My test for Fox's rule would be too liberal. We can evaluate each criticism.

If sparse species tend to generate assemblies with single guild members, then actual communities with three or more microtines should tend to represent non-Fox assemblies. In the plots, five microtine assemblies had three or more species, only two had a single member. Both zapodid species were present in 9 of the 12 assemblies. Fox's rule applied to three of the five speciose microtine assemblies. Neither sciurid was present in four of the non-Fox assemblies, even though their combined frequency (11) would allow single representation in all but one sample. In the transects, six assemblies had three or more microtines (but 3 had only 1). Only two of these assemblies obeyed Fox's rule. But both zapodids were present in seven assemblies, both sciurids were present in six. There was clear potential for the two zapodids and the two sciurids to exist in the richest communities. Nevertheless, all non-Fox assemblies had three or more microtines, but only one zapodid or sciurid.

What is the effect of ubiquitous deer mice (and nearly ubiquitous *Clethrionomys*)? I re-calculated the expected number of Fox assemblies by first excluding *Peromyscus* (53 possible communities with 1 or more species), then also excluding *Clethrionomys* (44 possible assemblies with 1 or more species). As expected, the probability of observing Fox assemblies, given the observed distribution of species richness, increased dramatically (from 0.03 to 0.13 and 0.18 respectively). But even in the most restricted model that excluded both *Peromyscus* and *Clethrionomys*, the probability of observing 13 or more Fox assemblies was highly significant ($P<0.001$).

Most ecologists would conclude that randomization using observed frequencies yields tests that are too conservative. Tests ignoring those frequencies may be too liberal. The conclusion depends critically on whether we believe that species either do, or do not, have equal opportunity to belong to any assembly. In the absence of definitive experiments, our assessment of whether all members of the community have equal access to each assembly must be based on the scale and replication of our observations relative to the community at large. For the small mammal assemblies that I analyze here, the scale is on the order of ten years and tens of square kilometers. The regional community from which those samples are drawn is, for both dimensions, at least an order of magnitude greater. The presence and absence of species in my local assemblies is clearly a product of their local dynamics and interactions, not their regional distribution.

What about the second question? What if sparse species are under-represented in my samples? Begging the indulgence of glib readers, we would not be playing with a full deck. But the "reduced" deck would be unbiased if sampling errors are equal for all individuals. Each species would be represented in proportion to its abundance and distribution in real assemblies. If trap bias is different among species, however, or if it depends on density, then some species would be over-represented while others are under-represented. The bias could influence the number of observed Fox and non-Fox assemblies. But the bias is unlikely to affect the analyses of whether more or less of those observed states can be generated by chance alone. Species would be redistributed from the biased deck.

Table A1. The presence (X) and absence (0) of different small mammal species captured over 12 years in eight 1 ha research plots in mature boreal forest in northern Ontario, Canada. Sampling intensity was not constant in all years. Note that each year had a unique assembly of species. One half of the rodent samples represent Fox assemblies (F), one half are non-Fox assemblies (NF).

Species	Year											
	1991	1992	1993	1994	1995	1997	1998	1999	2000	2001	2002	2003
	NF	F	F	F	F	NF	NF	F	NF	NF	NF	F
Bb	0	X	X	0	0	0	X	X	0	0	0	0
Cg	X	X	X	X	X	X	X	X	X	X	X	X
Mc	X	X	X	X	X	X	X	0	0	0	X	0
Mp	0	0	X	X	0	0	0	0	X	X	X	0
Ni	X	X	X	X	X	X	X	0	X	X	X	X
Pi	X	0	X	X	0	0	0	0	0	0	0	0
Pm	X	X	X	X	X	X	X	X	X	X	X	X
Sa	0	0	0	0	0	0	0	X	0	0	0	0
Sc	X	X	X	X	X	X	X	X	X	X	0	X
Syn	0	0	0	X	0	0	0	0	0	X	X	0
Tm	0	0	X	X	X	0	0	X	0	X	X	X
Ts	0	X	X	X	X	0	0	0	0	0	0	0
Zh	0	X	X	X	X	0	X	X	X	X	X	X

Bb = *Blarina brevicauda*, Cg = *Clethrionomys gapperi*, Mc = *Microtus chrotorrhinus*, Mp = *M. pennsylvanicus*, Ni = *Napaeozapus insignis*, Pi = *Phenacomys intermedius*, Pm = *Peromyscus maniculatus*, Sa = *Sorex arcticus*, Sc = *Sorex cinereus*, Syn = *Synaptomys cooperi*, Tm = *Tamias minimus*, Ts = *T. striatus*, Zh = *Zapus hudsonius*.

Table A2. The presence (X) and absence (0) of different small mammal species captured over 11 years along four 390 m transects in boreal forest in northern Ontario, Canada. Sampling intensity was not constant in all years. Each year had a unique assembly of small mammal species. Seven of the 11 rodent samples represent Fox assemblies (F), the others are non-Fox assemblies (NF).

Species	Year										
	1992	1993	1994	1995	1997	1998	1999	2000	2001	2002	2003
	NF	F	F	NF	F	F	F	NF	F	NF	F
Bb	X	0	0	0	0	X	X	0	0	0	X
Cg	X	0	X	X	X	X	X	X	X	X	X
Mc	X	0	X	0	0	0	0	X	0	0	0
Mp	X	0	X	X	X	0	0	X	X	X	0
Ni	X	0	X	0	0	X	0	X	X	X	X
Pi	0	0	X	0	0	0	0	0	0	0	0
Pm	X	X	X	X	X	X	X	X	X	X	X
Sa	0	0	0	0	0	0	X	X	X	0	0
Sc	0	0	X	X	0	X	X	X	X	0	X
Syn	0	0	0	X	0	0	0	X	X	X	0
Tm	X	X	X	X	X	X	X	X	X	X	X
Ts	0	0	X	X	0	X	X	0	X	0	X
Zh	X	0	X	X	X	X	X	X	X	X	X

Bb = *Blarina brevicauda*, Cg = *Clethrionomys gapperi*, Mc = *Microtus chrotorrhinus*, Mp = *M. pennsylvanicus*, Ni = *Napaeozapus insignis*, Pi = *Phenacomys intermedius*, Pm = *Peromyscus maniculatus*, Sa = *Sorex arcticus*, Sc = *Sorex cinereus*, Syn = *Synaptomys cooperi*, Tm = *Tamias minimus*, Ts = *T. striatus*, Zh = *Zapus hudsonius*.

Table A3. Trapping intervals used to assess small mammal communities living in eight 1 ha plots in a single stand of boreal forest (12 years), and along four 390 m transects (11 years). Periods correspond to bi-weekly census intervals commencing in mid May (period 1) and ending by mid September (period 9). An "X" indicates that a plot census was completed during that period. No census was completed in 1996. Single asterisks identify periods when both plots and (at least some) transects were trapped, double asterisks identify years when all transects were censussed.

Year	Periods								
	1	2	3	4	5	6	7	8	9
1991	X	X					X		
1992	X	X	X	X	X	X*	X*	X	X
1993	X*	X*	X	X	X	X	X	X	X
1994	X*	X*	X*	X*	X*	X	X*	X	
1995	X*	X*					X*		
1996									
1997		X	X*						
1998	X**	X**					X**		
1999				X**					
2000	X**	X**					X**		
2001	X**			X**					
2002	X**	X**					X**		
2003	X**	X**					X**		