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Synchrony in small mammal community dynamics across a forested landscape

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Long-term studies at local scales indicate that fluctuations in abundance among trophically similar species are often temporally synchronized. Complementary studies on synchrony across larger spatial extents are less common, as are studies that investigate the subsequent impacts on community dynamics across the landscape. We investigate the impact of species population fluctuations on concordance in community dynamics for the small mammal fauna of the White Mountain National Forest, USA. Hierarchical open population models, which account for imperfect detection, were used to model abundance of the most common species at 108 sites over a three year period. Most species displayed individualistic responses of abundance to forest type and physiographic characteristics. However, among species, we found marked synchrony in population fluctuations across years, regardless of landscape affinities or trophic level. Across the region, this population synchrony led to high within-year concordance of community composition and aggregate properties (e.g. richness and diversity) independent of forest type and low among-year similarity in communities, even for years with similar species richness. Results suggest that extrinsic factors primarily drive abundance fluctuations and subsequently community dynamics, although local community assembly may be modified by species dispersal abilities and biotic interactions. Concordant community dynamics across space and over time may impact the stability of regional food webs and ecosystem functions.

Across systems and taxa, long-term studies at local sites indicate that interannual abundance dynamics among trophically similar species tend to covary positively and that changes in abundance among species frequently are synchronized over time (Houlahan et al. 2007). Complementary studies examining synchrony in abundance among species across a landscape are less common, and when considered, emphasis generally is on exploitative or coupled interactions such as predator–prey dynamics (Moran 1953, Ims and Andreassen 2000, Fox et al. 2013) or host–parasite relationships (Grenfell et al. 2001, Cattadori et al. 2005). Yet, most systems are composed of multiple interacting species within a guild or taxonomic unit and the degree of synchrony in their abundance fluctuations will influence community dynamics, and stability in those dynamics, over time and space.

Concordance describes the degree to which communities, drawn from the regional species pool, covary positively over time and space. High community concordance across a landscape may be driven by parallel responses of species to extrinsic factors of resource quality or availability, climate perturbations, or wide-ranging predators (Liebhold et al. 2004). In such cases, the degree to which life history traits or functional traits are similar among species contributes substantially to community dynamics (Loreau and de Mazancourt 2008, Stange et al. 2011). For instance, communities composed of species in different feeding guilds or trophic levels will be more robust to temporal changes of resources than communities of species consuming only one resource type. Likewise, species-specific phenologies or overwintering strategies will differentially impact the ability of species to respond to predatory or environmental perturbations. Thus, across-site comparisons of species abundance dynamics and their aggregate community impact provides a powerful framework in which to evaluate the mechanisms structuring community dynamics (Stange et al. 2011, Michel et al. 2015). At the regional scale, this framework can also identify the role of habitat heterogeneity in shaping variability in community composition and aggregate properties of total abundance, richness, diversity, and evenness. Specifically, concordance across a landscape may be dampened by habitat heterogeneity which mediates competition among species and facilitates temporal stability of communities by providing greater refugia (Brown 2003). Understanding community concordance and the effect of habitat heterogeneity at the landscape scale has important implications for the structure and stability of food webs (Vasseur and Fox 2007, Gouhier et al. 2010) and for ecosystem function (Frost et al. 1995, Kent et al. 2007).

Small mammals (rodents and shrews < 250 g) are an excellent group for the study of community dynamics. They are diverse and are composed of members that vary considerably in their natural histories, often including a high degree of habitat and diet specificity (Reed et al. 2006, Stevens and Tello 2009, Stephens and Anderson 2014). Small mammals are also non-volant and are both short-lived and highly fecund, often producing multiple litters in one year (Egoscue et al. 1970). Subsequently, their populations are often more closely tied to local changes than those of more vagile animals, and their populations respond quickly to changes in climate and resource availability (Madsen and Shine 1999). These traits render small mammals especially well suited to the study of community concordance across large spatial scales such as a region. Moreover, because ecosystem functions provided by small mammals are largely dependent on species composition and numerical abundance, understanding dynamics at the regional scale may inform conservation and management efforts. In particular, small mammals are important vectors of zoonotic diseases (e.g. Lyme disease and Hantavirus; Ostfeld 1997, Yates et al. 2002) and can have profound effects on plant communities by directly consuming vegetation or insect pests and by dispersing seeds and mycorrhizal fungal spores (Maser et al. 1978, Jensen and Nielsen 1986, Andersen and Folk 1993).

Here we use small mammals in the White Mountain National Forest (WMNF) to investigate the impact of fluctuations of individual species on community concordance across a heterogeneous landscape. By simultaneously investigating species responses, community composition, and aggregate properties we can enhance understanding of the causes and consequences of variability and stability of communities across ecological scales (Micheli et al. 1999, Rowe et al. 2011, Supp and Ernest 2014). The WMNF small mammal assemblage is diverse, composed of both shrews (primarily insectivorous) and rodents (largely granivorous, fungivorous, or herbivorous). We modeled abundance of individual species over a 2100 km^2 expanse as a function of landscape variables and year while accounting for imperfect detection. Detection-corrected abundances of species were then compiled to examine spatial and temporal variability of communities over a three year period and across three dominant forest types. Our specific objectives were to 1) evaluate synchrony in abundance within and among multiple species relative to species traits and forest type, 2) determine the degree to which interannual dynamics in species abundance affect community composition and aggregate properties over space and time, and 3) determine the relative role of forest type and physiographic characteristics in structuring patterns of community similarity within and among years.

Methods

Study area

The White Mountain National Forest (WMNF) encompasses just over 3000 km^2 in north-central New Hampshire and western Maine, USA. The region is mountainous with elevations ranging from 115 to 1917 m. The climate is humid continental, characterized by warm summers and cold winters with a steep climatic gradient from valley bottoms to mountain tops. Precipitation occurs evenly throughout the year and increases with elevation (Dingman 1981). During the late 1800s and early 1900s much of the low- and mid-elevation forests were cleared, followed by widespread fires fueled by residual slash (Belcher 1980). Today, approximately 97% of the WMNF is forested and, as a result of regeneration, the majority of stands are between 90 to 130 yr old. Current localized disturbances include timber harvest, natural blow down, fungal pathogens, and ice damage. Low elevation mature forests are dominated by American beech *Fagus grandifolia*, sugar maple *Acer saccharum*, yellow birch *Betula alleghaniensis*, eastern hemlock *Tsuga canadensis*, and red spruce *Picea rubens*, whereas early- and mid-successional forests are composed of paper birch *B. papyrifera*, red maple *A. rubrum*, poplar *Populus* spp., and white pine *Pinus strobus* (Leak 1991). Balsam fir *Abies balsamea*, black spruce *Picea mariana*, and red spruce dominate higher elevations (800 m to 1450 m) beyond which the forest grades into alpine tundra (Leak and Graber 1974, Reiners and Lang 1979).

Small mammal trapping

During the summers of 1995, 1996, and 1997, the United States Forest Service (USFS) used a stratified sampling approach to survey small mammals at 108 sites (36 each year; a given site was only sampled once during the three years) across a 2100 km^2 expanse (Fig. 1). Elevation of sites ranged from 184 to 1092 m (mean 616 m) and cover types included hardwood ($n = 39$), mixed ($n = 40$), and softwood ($n = 29$) forests. Each site was sampled for 8 d in June and again in late July or August centered on the new moon phase (Prugh and Golden 2014). All sampling was removal sampling, and half of the sites ($n = 54$) were sampled using snap trap grids and the other half using pitfall trap arrays. A given snap trap grid was paired with a pitfall trap array, with sites averaging 90 m apart (Fig. 1). We accounted for this paired arrangement and difference in trap type by using 'location' as a random effect in our abundance modeling (see 'Abundance modeling'). Snap trap grids consisted of a 5 by 5 station arrangement with 10 m spacing among stations (Fig. 1). Each station had three small Victor snap traps and one Museum Special for a total of 100 traps per grid. Traps were baited with a mixture of peanut butter and rolled oats and placed within 1.5 m of the station. Pitfall trap arrays consisted of 10 pitfall traps (2.8 l) arranged along three drift fence wings (made from aluminum flashing) forming a Y-shape with a pitfall trap at the mid-point and one pitfall at each end (Fig. 1). An additional, isolated pitfall trap was placed at the centroid of each array. All traps were checked once daily for a total of 160 pitfall trap nights and 1600 snap trap nights for a given location. Collected animals were bagged, labeled, and frozen for later identification. Forest Service staff performed all sampling operations and procedures adhered to guidelines outlined by the American Society of Mammalogists (Sikes et al. 2011).

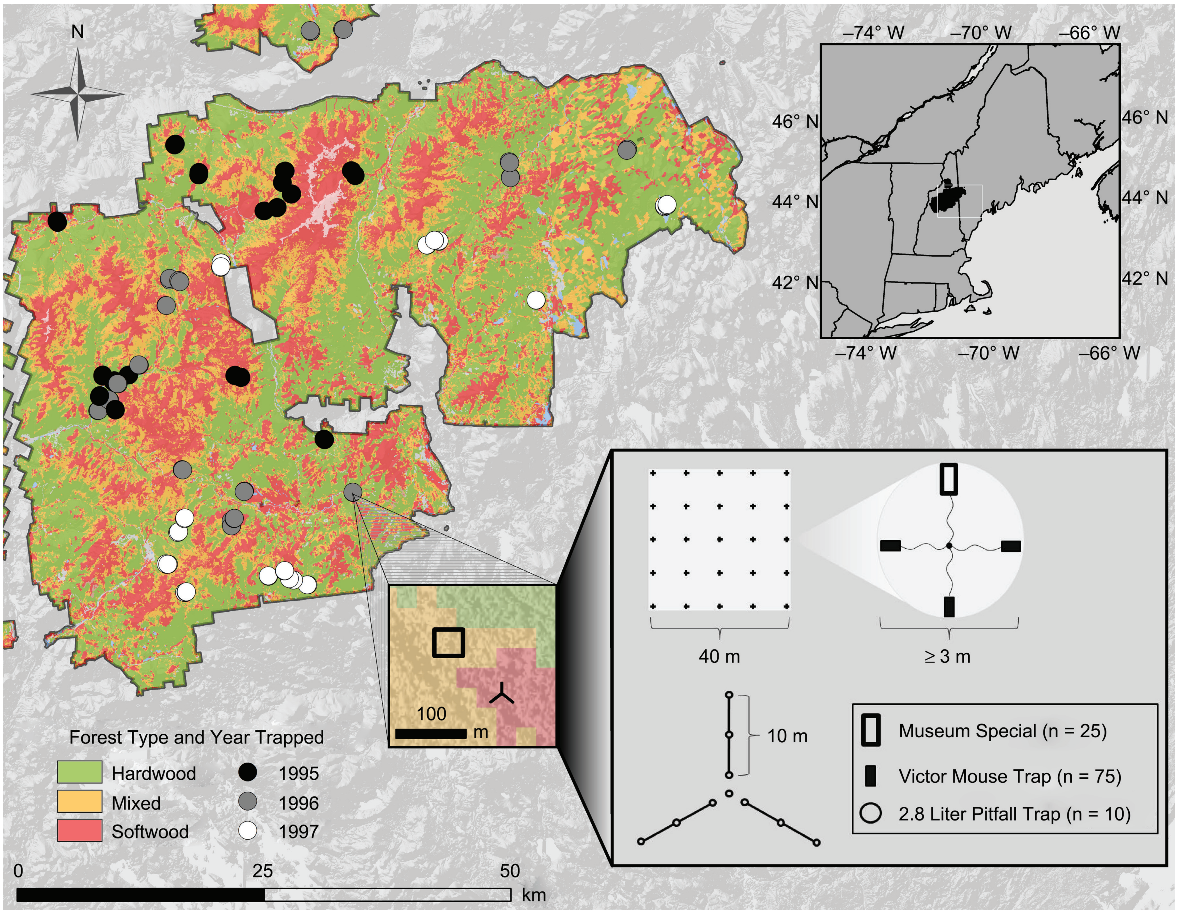

Figure 1. Distribution of sampling sites during the summers of 1995, 1996, and 1997 in the White Mountain National Forest, New Hampshire and Maine. In each year, 18 sites were trapped with snap trap grids and 18 with pitfall trap arrays. Snap trap grids consisted of 75 Victor snap traps and 25 Museum special snap traps. Pitfall arrays consisted of 10 – 2.8 l pitfall traps arranged along three drift fences (see inset).

Landscape variables

At each site we measured landscape variables likely to impact small mammal abundance. Within a 100 m buffer around each site, we used a GIS (ArcGIS ver. 10.1; ESRI, Redlands, CA, USA) to calculate physiographic characteristics (elevation and percent wetlands) and forest characteristics (percent forest cover type and age). Elevation was extracted from a digital elevation model (10 m resolution) obtained from the National Elevation Dataset (Gesch et al. 2002). We determined percent cover of wetlands or streams using the National Hydrologic Layer (Simley and Carswell 2009) with intermittent streams buffered by 2.5 m and perennial streams by 5 m. Wetlands and buffered streams were then merged into one layer and their area within each site buffer calculated. Forest cover type was derived from the 2001 New Hampshire Land Cover Data (NHLCD; <www.granit.unh.edu/>) and 2004 Maine Land Cover Data (MELCD; <www.maine.gov/megis/catalog/>; Smith et al. 2006). Using the majority rule in GIS, we resampled MELCD (5 m resolution) to match NHLCD (30 m resolution). Both data sets were reclassified into deciduous forest (hardwood), coniferous forest (softwood), mixed forest (mixture of deciduous and coniferous), and other. The proportion of hardwood, softwood, and mixed forest cover classes were assessed within each site buffer in FRAGTATS ver. 4.2 (McGarigal et al. 2002). Forest age was calculated as the difference between the year a site was trapped and the average of forest stands within a 100 m buffer, weighted by their relative area. Stand origin date was obtained from the WMNF forest stand layer (USFS, <www.fs.usda.gov/main/whitemountain/landmanagement/gis>) and represents the date a forest stand regenerated from a major disturbance (e.g. fire, hurricane, clear cutting) as estimated from a combination of early legal records, timber harvest sales, and tree cores. The accuracy of recent stand origin dates (<35 yr) were verified by overlaying orthophotos (1992) and digitized sale records provided by the USFS. Stands with no history of major disturbance (<7% of buffers by area) were assigned the year 1600, approximating the age of old-growth forests in the region (Leak 1974).

Abundance modeling

We used count data from small mammal trapping to model abundance for the 15 most common species (nine rodents and six shrews from a 22 species assemblage; Table 1).

Table 1. Captures of 22 small mammal species from 3 yr of sampling in the White Mountains National Forest, New Hampshire and Maine. A total of 108 sites were surveyed, with 36 sites trapped each year. Order is based on the rank abundance of the three-year total. Abundance analyses were conducted for species in boldface type.

	Year			
Species	1995	1996	1997	Total
Sorex cinereus	1731	372	872	2975
Napaeozapus insignis	234	781	698	1713
Myodes gapperi	1192	60	240	1492
Blarina brevicauda	302	14	631	947
Peromyscus maniculatus	529	31	149	709
Peromyscus leucopus	287	15	185	487
Sorex fumeus	77	23	44	144
Sorex hoyi	37	10	39	86
Microtus pennsylvanicus	20	2	22	44
Sorex dispar	25	3	11	39
Zapus hudsonius	18	10	7	35
Synaptomys cooperi	19	1	6	26
Tamias striatus	10	5	8	23
Sorex palustris	9	5	6	20
Microtus chrotorrhinus	3	2	13	18
Glaucomys sabrinus	4	2		6
Glaucomys volans	3	2	1	6
Tamiasciurus hudsonicus	4			4
Condylura cristata		1	2	3
Microtus pinetorum		1		1
Parascalops breweri			1	1
Synaptomys borealis		1		1
Total	4504	1341	2935	8780

A given site was trapped during one of the three years of sampling and we used these data to model abundance for all three years. Thus, detection-corrected abundance estimates were generated at each site for each species in 1995, 1996, and 1997. We validated our technique using an independent data set (see 'Model validation').

Using a hierarchical open population model within a Bayesian framework, we derived estimates of species abundance (λ), population change between sampling periods (γ), and probability of detection (p) from daily site captures from both June and late July/August sampling periods (Dail and Madsen 2011). Abundance in the first sampling period (June) was modeled as a function of covariates following a Poisson distribution with a log link,

$$N_{i,k=1} \sim Poisson\left(\lambda_{i,k=1}\right)$$

$$log\left(\lambda_{i,k=1}\right) = \beta_{1[l]} + \mathrm{B}_1 X_{1[i]}$$

where $N_{i,1}$ is the abundance in the first sampling period $k = 1$ at site i, $\lambda_{i,k=1}$ is the mean expected abundance as a function of parameters $X_{1[i]}$ including trap type, year, elevation, stand age, stream and wetland area, percent hardwood, and percent mixed forest type, which vary by site i. Expected abundance was also adjusted by an intercept, $\beta_{1[l]}$, which varied randomly by location l (i.e. paired snap trap grids and pitfall arrays). The Dail–Madsen model is a generalization of the N-mixture model for repeated counts (Royle 2004), but allows for open populations (i.e. emigration and immigration) between sampling locations and intervals while simultaneously accounting for imperfect detection. The open period (time between sampling) was modeled using an auto-regressive function,

$$\log\left(\gamma_{i,k=2}\right) = \alpha_l + \delta\left[N_{i,1} - \sum_{j=1}^{J} y_{i,j,k=1}\right]$$

where $\gamma_{i,k=2}$ is the mean expected abundance in the second survey period (late July/August) over all sample nights J, α_l is an intercept that varies randomly by location, and δ is the change in abundance from the end of the first survey to the start of the second survey. Because individuals were permanently removed during the first period, δ is multiplied by the abundance at the end of the first period ($N_{i,1}$ less the number of individuals removed, $\sum_{j=1}^{J} y_{i,j,k=1}$, during sampling). The abundance in the second survey period at site i is again assumed to follow a Poisson distribution:

$$N_{i,k=2} \sim Poisson\left(\gamma_{i,k=2}\right)$$

We modeled change in abundance rather than separating apparent survival and recruitment, as described by Dail and Madsen (2011), because we lacked long time series with multiple open periods needed to distinguish the additional parameters.

Our modeling technique also explicitly accounted for imperfect detection. In the detection model, counts followed a multinomial distribution because individuals were removed from the population during sampling. The multinomial had eight categories, one for each survey night during the closed (i.e. sampling) period. Because the number of animals in the population decreased by the number of captures the previous night, probability of capture was adjusted accordingly,

$$y_{i,j,k} \sim Multin\left(N_{i,k}, P_{i,j=1:8,k}\right)$$

where $y_{i,j,k}$ is the observed number of captures at site i on sample night j, during survey period k and $p_{i,j,k}$ is the associated probability of detection. The probability of capturing an individual may be affected by extrinsic parameters including environmental conditions (precipitation, minimum daily temperature, and minimum daily temperature^2) or trapping technique (snap trap and pitfall trap) and was therefore adjusted following a regression sub-model with a logit link,

$$logit\left(p_{i,j,k}\right) = \beta_{2[l]} + \mathrm{B}_2 X_{2[i,j,k]}$$

where $\beta_{2[l]}$ is an intercept that varies randomly by location l, B_2 is the vector of coefficients to be estimated, and $X_{2[i,j,k]}$ is the independent data matrix of parameters that vary by site, sample night, and survey period. Trap type was included in both the detection and abundance portion of the model because it can affect the probability of catching an animal (detection) and the abundance of a species (i.e., snap trap grids and the pitfall arrays may sample different size areas and hence different population sizes). At the site level, we used PRISM climate data (PRISM Climate Group, <www.prismclimate.org>) at 4 km resolution in GIS to extract daily minimum temperature and precipitation that occurred while traps were open. We considered trap type as a binary covariate (0 = pitfall, 1 = snap trap).

The open population model was implemented in JAGS (Plummer 2003) via R 3.1.2 software (R Development Core Team) using the package rjags (Plummer 2013). JAGS uses Markov Chain Monte Carlo (MCMC) methods, with a Gibbs sampler, to generate posterior distributions for model parameters. We ran three parallel chains of 100 000 iterations each, discarded the first 50 000 to avoid effects due to random starting values and thinned by 25. This left 6000 iterations (2000 per chain) to construct the posterior distribution. We chose non-informative priors to ensure that our inference was driven by the data. Specifically, we used a normal distribution with a mean of 0 and standard deviation of 10 (formulated as precision in JAGS; Plummer 2003) for all abundance covariate coefficients and uniform priors of –3 to 3 for all detection coefficients. For hyperpriors (standard deviation) of the random effects, we used uniform priors of 0 to 5 for population change and 0 to 10 for location effects on abundance. All continuous variables were z-standardized prior to analysis (i.e. subtracting the mean and dividing by the standard deviation). Model fit for each species was assessed using posterior predictive checks by visually comparing observed count data to posterior predicted count data generated from the model and ensuring that the Bayesian p-value of chi square test was near 0.5 (between 0.25 and 0.75; Kéry 2010). The effect of a given variable on a species' abundance was interpreted as significant if zero was not included within 95% credible intervals. Code for implementing the model is available at: <https://github.com/djhocking/Small_Mammal_Synchrony>.

Model validation

Because our abundance and community analyses took advantage of model data both from years that were trapped and those that were not trapped, we used an independent data set from Bartlett Experimental Forest (BEF), central WMNF, to validate model predictability. These small mammal capture data came from four pitfall trap arrays (same setup as the regional sampling but without paired snap trap grids) in hardwood forest sites. Sites were surveyed in the same three-year period (each site surveyed 1995, 1996, and 1997) during which the WMNF dataset was collected, but were not included in the regional assessment.

To assess predictability, we ran our model for each species where one year of count data from the BEF sites, randomly selected for each site, was used to predict abundance for the other two years (predictions from training data). We then reran the model with all three years of BEF count data and estimated the abundance at each site and year to form a validation dataset. Both series of models used landscape variables, detection variables, and the three years of WMNF small mammal count data to derive abundance. For the six most common species, we assessed the models' ability to predict a species' abundance by using a Pearson's correlation between predicted abundance (using the training data) and expected abundance (from the model which included all validation data). Additionally, we assessed the effect of using predicted species abundance on community composition (see Community validation section).

Community properties and similarity

Using detection-corrected abundance data for the 15 most common species in the WMNF dataset, we quantified the following community properties of each site: total abundance (number of individuals across all species), richness (S = total number of species), diversity (Shannon Wiener index; $H' = -\Sigma\ p_i \ln[p_i]$, where p_i is proportional contribution of the ith species), and Pielou's evenness index ($J = H'/\log[S]$). We separately compared abundance, richness, diversity, and evenness across years within a forest type using a Friedman test (non-parametric repeated measures) and pairwise Wilcox tests to determine which years were different. We used a Kruskal–Wallis test and pairwise Wilcox tests for each metric within a year to determine if community properties differed by forest type. Non-parametric analyses were chosen due to deviations from normality within some groups.

We used a Bray Curtis dissimilarity matrix generated from detection-corrected abundance data for the 15 most common species to assess the effect of year and landscape variables on compositional similarity. To visualize trends in small mammal compositional similarity among years and forest types we used non-metric multidimensional scaling (NMDS), a robust unconstrained ordination method. Additionally, to facilitate comparison of our results to other studies, we complemented the NMDS with a similarity matrix. Matrix values were the mean pairwise Bray Curtis similarity (1 – Bray Curtis dissimilarity) of sites within and among forest types and years. We used PERMANOVA (multivariate repeated-measures ANOVA – function 'adonis' in R package Vegan; Oksanen et al. 2014) to quantify the role of year, forest type, and physiographic characteristics in structuring small mammal compositional similarity. We also tested for an interaction of year and forest type. We applied the repeated measures by using site as the nesting factor and assessed significance through comparisons with 999 randomized data sets. In balanced sampling designs such as ours (i.e. same number of sites in each year), PERMANOVA can differentiate between location vs dispersion effects, making it well suited for detecting differences in community similarity among sampling units (Anderson and Walsh 2013). When we detected a significant main effect of year, we conducted pairwise comparisons to determine which years had significantly different community composition. Significance levels were adjusted with Holm's correction for multiple comparisons (Holm 1979).

We assessed the effect of distance between sites on community similarity using Mantel tests. Within each forest type, in a given year, we assessed correlation between matrices of community similarity (Bray Curtis) and linear distance (km). If community similarity decreased with increasing linear distance we expected a significant p-value and the Mantel r statistic to have a negative slope. Mantel tests were performed using R package Vegan, and significance was assessed with a Monte-Carlo procedure with 999 permutations (Oksanen et al. 2014).

To determine if variation in community similarity differed among years or forest types within a year, we used the function 'betadisper' from R package Vegan (Oksanen et al. 2014). This analysis of dispersion compares the mean distance of group members to the group centroid, in this case year or habitat, and we interpreted results as a measure of relative concordance of communities across the landscape (lower multivariate dispersion = higher concordance). When significant, we used Tukey's post hoc tests between years or forest types within a year to determine pairwise differences.

Community validation

Our community level assessment of the WMNF sites used predicted abundance data and we tested the sensitivity of using these estimates in compositional similarity analyses by using our BEF model validation dataset. We used an NMDS to compare community composition of each BEF site using abundances modeled from one year of observed count data (training set) to the community composition of the same BEF site in the same year using abundance data derived from a model with all three years of observed count data (validation set). Additionally, we tested if predicted abundance may have biased our community results within the WMNF dataset. We used a PERMANOVA (applied without the repeated measures), for each year, to assess if community similarity calculated from WMNF sites which were trapped in that year differed from sites which were not trapped that year (predicted abundance).

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.76jr5> (Stephens et al. 2016).

Results

Abundance of species

Over the three years, the USFS collected 8780 individuals represented by 22 species from across 108 locations (Table 1). We modeled abundance as a function of detection and landscape variables for the 15 most common small mammal species (> 99.7% of total captures; Table 1, Fig. 2). Our model validation procedure indicated that our abundance modeling approach provides appropriate estimates for individual species (see 'Model validation' below). Detection variables (trap type, precipitation, temperature, and temperature^2) were important in explaining heterogeneity of abundance for 10 species (Fig. 2). We described abundance variables in terms of trap type and landscape features including forest characteristics (age and forest type) or physiographic characteristics (elevation and percent wetlands). Trap type affected abundance for six species with a general trend of snap traps capturing more rodents and pitfall traps capturing more shrews. Of the landscape variables, forest characteristics were significant for six species and physiographic characteristics significant for four species (Fig. 2). The effect of year (relative to 1995) on abundance was significant for seven species in 1996 and six species in 1997 (Fig. 2).

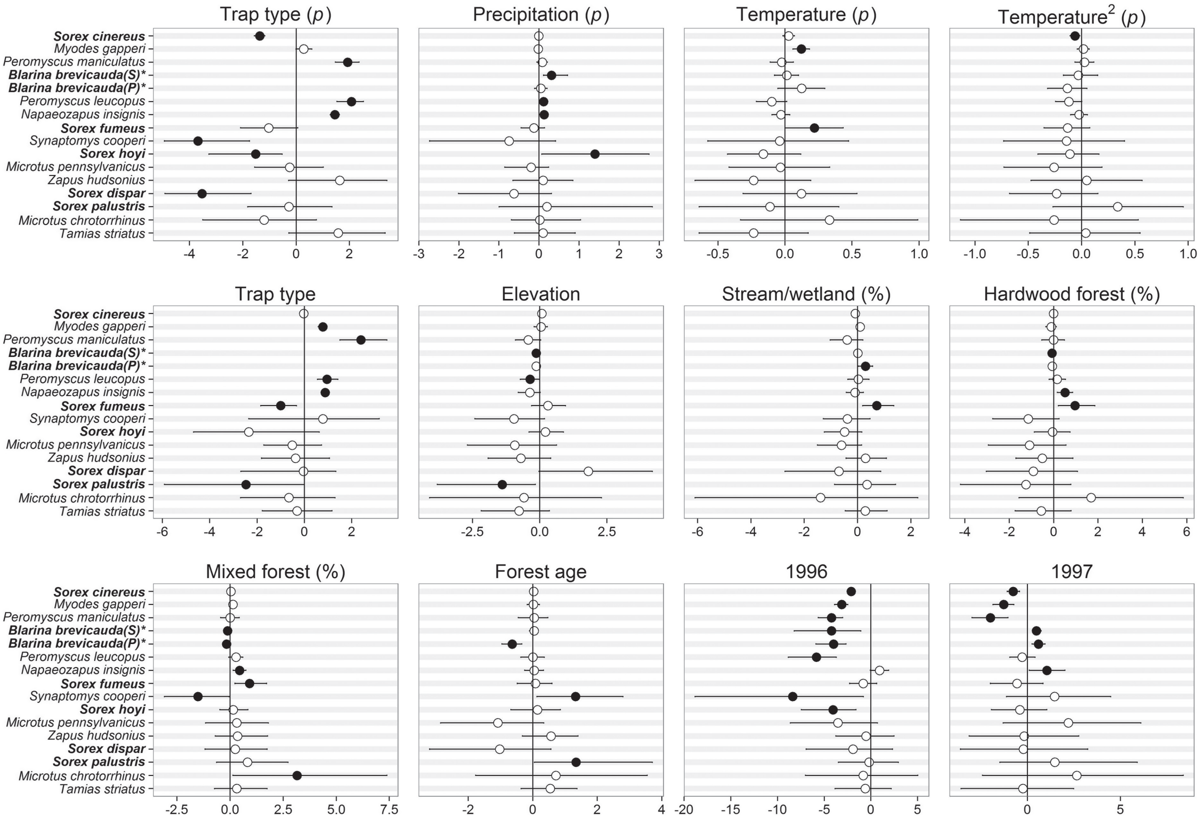

Figure 2. Results of an open population hierarchical model analyzed within a Bayesian framework for the 15 most abundant small mammal species. Species were modeled separately and are arranged from top to bottom in order of descending modeled abundance for 1995. Shrews are indicated in boldface type. Detection variables are indicated by (*p*). Circles indicate mean response in abundance or detection and error bars represent 95% credible confidence intervals. Closed circles indicate parameters for a species that do not contain zero within 95% credible intervals. The effect of hardwood and mixed forest is relative to softwood forest and the effect of 1996 and 1997 are relative to 1995. Positive values for trap type indicate an increased response to snap trap whereas negative values indicate an increased response to pitfall traps. **Blarina brevicauda* were modeled separately for snap trap captures (S) and pitfall captures (P) due to non-convergence when abundance was modeled simultaneously.

Six species comprised $>95\%$ of the small mammal community (Fig. 3). Five of these dominant species showed great synchrony in response, displaying similar abundance changes across years with a dramatic decrease from 1995 to 1996 and then an increase from 1996 to 1997 (Fig. 3). The exception was the woodland jumping mouse *Napaeozapus insignis* which increased in abundance during 1996 and remained high during 1997 (Fig. 2, Fig. 3). Abundance trends were consistent across years irrespective of diet (i.e. insectivore, granivore, or herbivore; Fig. 3). Moreover, although the magnitude of a species response varied across forest types, the overall patterns did not (Fig. 3).

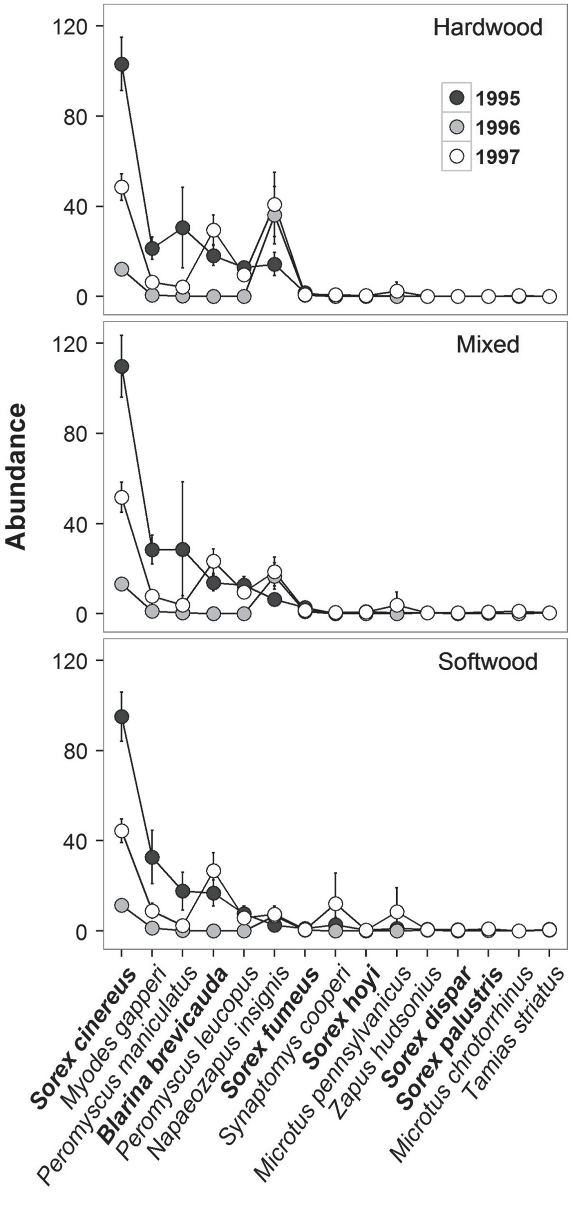

Figure 3. Mean site abundance as calculated from detection corrected abundance estimates for the 15 most common small mammal species at 108 sites in the White Mountain National Forest, New Hampshire and Maine. Plots are arranged by forest type: hardwood (top), mixed (middle), and softwood (bottom). Circles represent mean abundance for a given year and bars indicate 95% confidence intervals. Species are arranged from left to right in order of descending modeled abundance during 1995. Shrews are indicated in boldface type.

Model validation

Using our independent data from BEF we found agreement between abundance predicted during two of the years and abundance estimated from all three years of trap data. Both abundance estimates were highly positively correlated for five of the six species (Pearson's $r = 0.83$ to 0.99; Supplementary material Appendix 1, Fig. A1), with the exception of the southern red-backed vole *Myodes gapperi* ($r^2 = 0.23$), a species that was captured at very low abundances in BEF. Although our model tended to slightly under-predict higher abundances (Supplementary material Appendix 1, Fig. A1), this result was minor and consistent across species and years, which likely is why predicted abundance had no observable influence on community metrics (see 'Community validation'). Importantly, our BEF validation data come from one area and thus the observed pattern of under-predicted higher abundance likely indicates site-specific shrinkage toward the mean, such that other sites would slightly over-predict. Together, these findings indicate that our open population model yielded robust estimates of abundance, even for years when trapping did not occur at a site.

Community properties and similarity

We quantified community properties in terms of abundance, richness, diversity, and evenness. These metrics differed across years, but were largely unaffected by forest type (Fig. 4). Mean site abundance was significantly different across all years with higher abundance in 1995 than 1997, and exceptionally low abundance in 1996. Abundance was the only metric that differed by habitat within a year and was higher in hardwood and mixed sites compared to softwood sites in 1996. This trend was likely due to the dominance of *N. insignis* in 1996 and its strong habitat affinity toward hardwood forests (Fig. 2, Fig. 3). Site richness was significantly affected by year, with less than half the number of species present in 1996 compared to either 1995 or 1997. Diversity was significantly different across all years and was highest in 1997 and considerably lower in 1996. Evenness was consistent across years with slight differences noted in mixed forest types between years.

At the regional scale, small mammal community composition was significantly affected by year and landscape characteristics (Table 2). However, year explained 50.9% of variation in community composition whereas forest and physiographic characteristics only explained a small portion of variation: forest type (4.0%), elevation (1.1%), percent stream/wetland ($<0.1\%$), and forest age ($<0.1\%$). The interaction of year and forest type was not significant, indicating that although communities changed across years, the relative effect of forest type stayed consistent (Table 2). Pairwise PERMANOVA comparisons between years indicated that each year had significantly different community composition: 1995 vs 1996 ($F_{1,210} = 300.00$, adj. $p = 0.003$), 1996 vs 1997 ($F_{1,210} = 164.76$, adj. $p = 0.003$), and 1995 vs 1997 ($F_{1,210} = 69.99$, adj. $p = 0.003$); however,

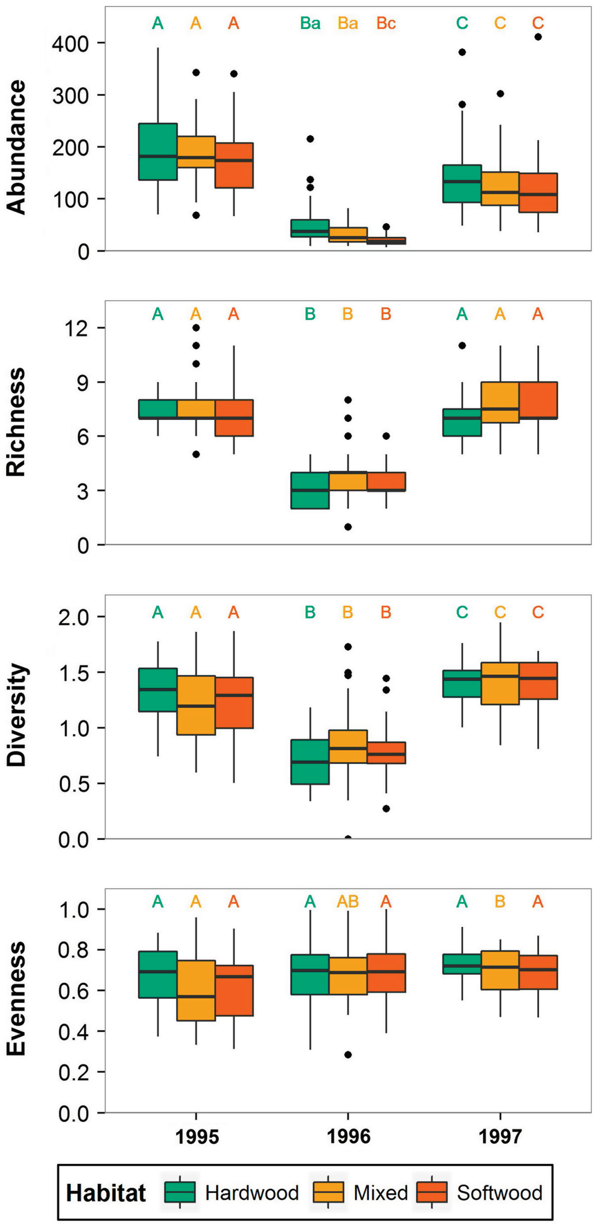

Figure 4. Box-and-whisker diagrams of four community metrics (abundance, richness, diversity, and evenness) for small mammals in hardwood, mixed, and softwood forests during each of the three survey years. Capital letters denote significant differences of a metric across years within a forest type based on Friedman tests and pairwise Wilcox tests, and lowercase letters denote significant differences between habitats within a year based on Kruskal–Wallis tests and pairwise Wilcox tests (only indicated for years with significant differences). Boxes with the same letters are not significantly different, whereas different letters indicate a significant difference. Corresponding test statistics for Friedman tests and Kruskal–Wallis tests can be found in Supplementary material Appendix 1, Table A1 and A2, respectively.

Table 2. PERMANOVA analysis showing the effect of year and physiographic characteristics on small mammal community composition across 108 sites. Distance among small mammal communities is based on a Bray Curtis dissimilarity matrix generated from detection-corrected abundances for the 15 most common species. We applied repeated measures by using site as the nesting factor.

Factor	DF	*F*-value	R^2	p
Year	2	188.865	0.5087	0.001
Forest type	2	14.738	0.0397	0.001
Elevation	1	8.260	0.0111	0.001
Stream/Wetland (%)	1	3.941	0.0053	0.001
Forest age	1	4.551	0.0061	0.001
Year × Forest type	4	1.639	0.0088	0.155
Residuals	312		0.4202	

year explained 56.1% of variance in community composition between 1995 and 1996 whereas it explained only 23.7% from 1995 to 1997 and 40.9% from 1996 to 1997. These trends were readily apparent in the NMDS ordination with strong clustering of communities by year along axis 1 and weak clustering by forest types within years along axis 2 (2 dimensions, stress = 0.119; Fig. 5A, B). Furthermore, based on Bray Curtis similarity, local communities were more similar across forest types within a year (0.58–0.70) than across years within a forest type (0.37–0.55; Fig. 5B, C). Within a year, there were no statistically significant correlations between linear distance of sites (avg. 26.8 km) and community similarity (Bray Curtis similarity) across a forest type (Table 3).

We detected significant differences in the degree of community similarity, or concordance, among years ($F_{2,321} = 15.85$, $p < 0.001$). Tukey's post-hoc testing revealed that concordance was significantly higher in 1995 than in 1996 ($p < 0.001$) or 1997 ($p = 0.003$), and although there was not a significant difference between 1996 and 1997 ($p = 0.059$), there was a trend of 1996 having lower concordance than 1997. Differences in concordance among years were also visible in the NMDS plot with a greater spread among points in 1996 and 1997 compared to 1995 (Fig. 5A). Community concordance did not differ among forest types within a year: 1995 ($F_{2,105} = 0.222$, $p = 0.802$), 1996 ($F_{2,105} = 2.007$, $p = 0.150$), and 1997 ($F_{2,105} = 0.563$, $p = 0.583$).

Community validation

Similar to our species-level model validation, community trends were not biased by using model-predicted abundance data from years that were not trapped. Within a year, an NMDS ordination of BEF communities using all three years of observed count data to estimate species abundances aligned with communities using just one year of data to estimate species abundance (Supplementary material Appendix 1, Fig. A2). Additionally, both fell well within the yearly variation of the WMNF communities (Supplementary material Appendix 1, Fig. A2). Among WMNF sites, there were no differences in composition when comparing communities with abundance from the year a site was trapped to communities with predicted abundance (years a site were not trapped) in 1995 ($F_{1,106} = 1.165$, $p = 0.312$), 1996 ($F_{2,106} = 1.54$, $p = 0.210$), or 1997 ($F_{1,106} = 0.98$, $p = 0.418$). This was also apparent in the NMDS ordination with all communities, within a year, clustering within the

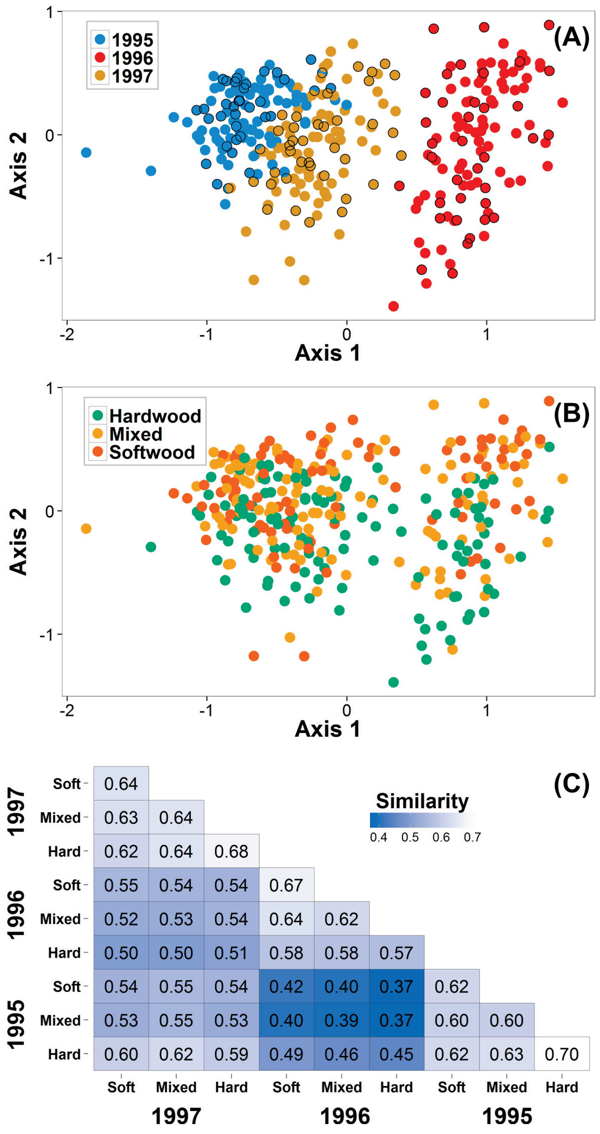

Figure 5. Similarity among small communities by forest type and year. Panels (A) and (B) are a two-dimensional nonmetric multidimensional scaling ordination of the 108 sampling sites over the 3 sampling years (324 total communities). Increased pairwise distance between sites (circles) indicates decreased similarity of community composition. Overlays represent small mammal community relationships with year (A) and forest type (B). The relative spread of sites within these categories can loosely be interpreted as the degree of community concordance. Outlined circles (A) represent communities composed of abundance data from sites which were trapped in that year, whereas circles without an outline represent communities composed of model predicted species abundance data (i.e. sites were not trapped in that year and species abundance data were predicted based on landscape variables, detection variables, count data from other sites trapped during that year, and count data from the year it was trapped). Panel (C) is a heat diagram of pairwise Bray Curtis similarity values (where 0 = completely dissimilar and 1 = identical) between forest types and years. Larger numbers and lighter colors indicate more similar communities. Abbreviations refer to forest type: Hard (hardwood, n = 39), Mixed (mixed, n = 40), and Soft (softwood, n = 29).

same space (Supplementary material Appendix 1, Fig. A2), further supporting our use of predicted abundance data in our community analyses.

Table 3. Results of Mantel tests comparing small mammal community similarity (Bray Curtis) and linear distance (km). Significance of Mantel tests was based on 999 permutations.

Forest type and year	Mantel r	p
Hardwood (1995)	0.0197	0.453
Hardwood (1996)	–0.1064	0.902
Hardwood (1997)	–0.0125	0.615
Mixed (1995)	–0.0535	0.796
Mixed (1996)	–0.2555	0.998
Mixed (1997)	–0.1930	0.986
Softwood (1995)	–0.2853	1.000
Softwood (1996)	–0.2614	0.999
Softwood (1997)	–0.2797	1.000

Discussion

For most species, we detected individualistic responses of abundance to forest or physiographic characteristics. However, among species, we found marked synchrony in population fluctuations across years, regardless of trophic level or landscape affinities. These parallel shifts in abundance led to largely concordant regional community dynamics within a year. At the community level, total abundance, diversity, and richness were similar among forest types within a year, but were significantly different within a forest type among years. Overall, year explained more than 50% of variation in community composition, whereas forest and physiographic characteristics collectively explained only 6% of variation. Studies at smaller spatial scales in the northeastern US have found similar trends with interannual abundance of species fluctuating synchronously across forest types, successional states, and elevation (DeGraaf et al. 1991, Brooks et al. 1998).

Growing evidence suggests that broad-scale community concordance may be common in many systems. For example, within Lepidoptera (Stange et al. 2011) and bacterioplankton (Crump and Hobbie 2005, Kent et al. 2007, Andersson et al. 2010) communities, abundance dynamics among taxa are consistently shown to be synchronized, even at the hemisphere-scale (Myers 1998, Crump et al. 2009). In small mammals, it is unclear how pervasive landscape concordance is among communities. Synchrony in population dynamics of small mammal species is common (Krebs and Myers 1974) and has been observed among species feeding at similar trophic levels (e.g. herbivorous arvicoline rodents; Krebs et al. 2002). Few studies have investigated landscape concordance among small mammal communities composed of species that vary in their natural histories (but see Korpimäki et al. 2005). Species-specific differences in ecological traits, in particular diet, may render idiosyncratic responses of species across a resource gradient or in response to punctuated availability of a resource type such as masting or insect outbreaks. Based on this assumption, one might expect asynchrony in community dynamics across a heterogeneous landscape. Yet, despite differences in forest type and physiographic characteristics and an assemblage composed of species with diverse natural histories, we demonstrate overwhelming similarity in community composition and structure across the region.

The WMNF small mammal assemblage is composed of species which are insectivores, granivores, fungivores, or herbivores (DeGraaf and Yamasaki 2001). Abundance dynamics of these species tracked similarly across forest types within a year, irrespective of diet, indicating that limiting food resources were likely not responsible for the observed synchrony. Rather, extrinsic factors likely caused the synchronous abundance dynamics we observed. Of the 15 most common species, only one showed a positive increase in abundance between 1995 and 1996. This species, the woodland jumping mouse, is the only obligate hibernator, suggesting a role in overwintering strategy in structuring its response. Merritt et al. (2001) also found population growth rates of woodland jumping mice to be inversely correlated with other small mammal species. This suggests extrinsic factors may have been acting on small mammal communities during the winter of 1995–1996 and that hibernation buffered woodland jumping mice from this perturbation. In studies of arvicoline rodents (voles and lemmings), multispecies synchrony in abundance is often driven by extrinsic factors of climate and predation (Hanski and Korpimaki 1995, Huitu et al. 2008). For overwintering populations, extreme climatic events during the winter or early spring may have disproportionately large adverse effects on population dynamics if resources are already limited (Hansen et al. 2013). Interestingly, lepidopteran dynamics are often synchronized across the WMNF (Stange et al. 2011), demonstrating that other groups may have similar responses to extrinsic factors such as climate.

Along with widespread synchronous declines of abundance from 1995 to 1996, we also observed a 50% loss in local species richness. In 1997 site richness was similar to 1995; however, community composition was markedly different and more variable, suggesting that dramatic synchronous declines permit the re-assembly of communities year to year and that dispersal plays a large role in structuring community composition (Thibault and Brown 2008). Comprehensive data on dispersal capacities for species in the region are lacking; nonetheless, body mass ranges from 2.9 ± 0.6 g (pygmy shrew *Sorex hoyi*) to 76.7 ± 10.0 g (eastern chipmunk *Tamias striatus*), suggesting that dispersal should vary considerably among species (Etienne and Olff 2004). Differences in dispersal contribute to colonization potential and the demographic success of species (Clobert et al. 2012). Furthermore, timing of colonization and its coincidence with availability of resources or the abundance of competitors also contribute to a species ability to occupy a site (Davis et al. 2000, Shea and Chesson 2002). These processes may have led to the large variation in community composition among sites in 1997 compared to 1995, despite similar species richness. The greater similarity among communities during years of high abundance (i.e. 1995 compared to either 1996 or 1997 and a trend of 1997 being more concordant than 1996) may indicate that small mammals in the WMNF region operate under source-sink metacommunity dynamics. As local abundance increases in high quality patches, individuals disperse to lower quality patches (Matthysen 2005). At the species level, such density dependent dispersal may partially explain the relatively weak individualistic responses of species to physiographic characteristics compared to the year effect we observed. At the community level, high dispersal would homogenize the metacommunity (Mouquet and Loreau 2003), which may reflect the high concordance among communities we observed in 1995.

Overall, our observations raise the question of whether the WMNF landscape is indeed heterogeneous – at least as perceived by small mammals. Although three forest types are dominant (i.e. hardwood, softwood, and mixed), these forests have all regenerated from extensive clearing over a century ago, making them approximately even-aged. Thus, the region may superficially appear heterogeneous in forest type but may be homogenous with respect to structural complexity and resource availability, providing equal refuge among a suite of small mammal species that may otherwise discriminate (Lovejoy 1975, DeGraaf et al. 1991). Similar anthropogenic homogenization of forests in the western United States has ostensibly lowered local species richness (by selecting for generalist species) which subsequently reduced the complexity of the small mammal community (Kelt et al. 2013). In our study, forests averaged 119 (± 65) yr old and only 6% of sites were < 50 yr of age. Forest age was not an important predictor of abundance for the six most common species, but rarer species tended to trend characteristically toward either older or younger forests (Fig. 2). In the WMNF, disturbances prior to intensive human land use consisted of fires and wind-throw, creating temporally intermittent and patchy forest openings of variable size embedded within a matrix of mature forest (Foster 1988, Cogbill 2000). Management strategies that retain mature forests and create a mosaic of forest clearings of early successional habitat across the landscape may emulate historical disturbances and promote greater biodiversity (North et al. 2009, North 2012). These management practices would maintain vertical complexity that accompany older forests and forest openings would increase habitat for uncommon early successional species such as the meadow vole *Microtus pennsylvanicus*, ultimately increasing β-diversity across the landscape (Welsh and Healy 1993, Costello et al. 2000). Additionally, local studies investigating the effects of timber management on dominant small mammals in the WMNF indicate that the abundance of woodland jumping mice responds positively to structure associated with regenerating forest whereas abundance of deer mice *Peromyscus maniculatus* responds positively to characteristics associated with older forests (Lovejoy 1975, DeGraaf et al. 1991). Thus, the resultant heterogeneity of forest structure across the landscape may lead to greater partitioning among the more common forest dwelling species, ultimately reducing concordance of community dynamics (Brown 2003).

Given the importance of small mammals as critical prey and consumers in forested ecosystems (DeGraaf and Yamasaki 2001), community concordance may have implications for ecosystem structure and function. Particularly within the WMNF region, declines in species richness and aggregate abundance across the landscape could generate time-lagged fluctuations of predators specializing on small mammals such as the American marten *Martes americana* (Thompson and Colgan 1987). Moreover, the parallel loss of species feeding in multiple trophic guilds indicates a cumulative reduction of ecosystem functions including consumption and dispersal of seeds, dispersal of mycorrhizal fungal spores, and regulation of arthropods. The lack of compensatory dynamics (sensu Houlahan et al. 2007) we document among the WMNF small mammal species may indicate that competition is less important than extrinsic factors in structuring community composition and dynamics in the region. However, differences in dispersal coupled with competition may be important for assembling local communities following broad scale synchronous declines. Future research will benefit from analyzing long-term dynamics of small mammal communities in the region to determine the role of competition, exogenous factors, and forest structure in generating the community structure and dynamics we observed.

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Supplementary material (Appendix ECOG-02233 at <www.ecography.org/appendix/ecog-02233>). Appendix 1.