

Research Article

Drivers of small mammal population dynamics in hardwood forests of northeastern USA

Joshua S. Willems¹, Remington J. Moll¹, Mariko Yamasaki², Christine Costello², Mark J. Ducey¹, Rebecca J. Rowe¹

¹University of New Hampshire, Natural Resources and the Environment, 114 James Hall, 56 College Road, Durham, NH 03824, United States

²Forest Sciences Laboratory, US Department of Agriculture Forest Service, Northern Research Station, 271 Mast Road, Durham, NH 03824, United States

*Corresponding author: University of New Hampshire, Natural Resources and the Environment, 114 James Hall, 56 College Road, Durham, NH 03824, United States.

Email: Joshua.Willems@unh.edu

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Abstract

Many small mammal populations exhibit dramatic annual fluctuations, with abundance sometimes varying by orders of magnitude across years. However, there remains much debate about the factors that drive changes in abundance. Long-term datasets provide important opportunities to further investigate these phenomena. Using 30 yr of data from a study at Bartlett Experimental Forest in north-central New Hampshire, USA, we compare the relative effects of pulsed food resources (beech mast), forest structure, and weather on the population dynamics of 5 rodents and 4 shrew species. We estimated detection-corrected abundances using Bayesian *N*-mixture models. Mast, forest structure, and weather all influenced abundance; however, responses varied among species, and no single variable proved to be broadly influential across all species. More generally, our results suggest that for most species analyzed, mast availability and weather patterns have a greater influence on abundance fluctuations than forest structure. However, our results suggest that species are not responding to changes in the environment in the same way. Given that small mammals are ubiquitous and serve key ecological roles, a better understanding of the drivers of small mammal population fluctuations could have broad-reaching implications for forest ecology and management.

Key words: cycle, forest structure, long-term monitoring, mast, *N*-mixture model, northern forest, population density, resource pulses.

Many species of small mammals (rodents and shrews) exhibit dramatic interannual fluctuations in population size (reviewed in [Andreassen et al. 2021](#)). Across species and systems, studies have shown that a variety of factors can contribute to interannual fluctuations in population size including predator/prey dynamics ([Blackwell et al. 2001](#); [Klemola et al. 2002](#)), disease outbreaks ([Boonstra et al. 1998](#); [Smith et al. 2008](#)), fluctuations in resource availability ([Ostfeld et al. 1996](#); [Ostfeld and Keesing 2000](#); [Falls et al. 2007](#)), changing weather patterns ([Dhawan et al. 2018](#)), and habitat disturbance ([Fantz and Renken 2005](#); [Boggs et al. 2020](#)). Despite this large body of work, there remains uncertainty around the relative importance of and potential interaction between these factors. This question is further complicated by the need to tease apart short-term population responses from multiannual or multidecadal trends, which often requires long-term datasets ([Deitloff et al. 2010](#)). Maintaining long-term monitoring projects, however, can be challenging due to their logistical demands and costs. Many studies on small mammal population dynamics have either examined changes across a relatively short time period (i.e., 2 to 5 yr; e.g., [Fantz and Renken 2005](#); [Kellner et al. 2013](#)) or focused on only a few species ([Elias et al. 2004](#); [Deitloff et al. 2010](#); but see [Thibault et al. 2010](#); [Kellner et al. 2019](#)). As such, analyzing long-term population trends of multiple species is needed to develop a robust understanding

of the drivers of population fluctuations and the degree to which responses are synchronized among species.

Identifying the underlying drivers of small mammal population fluctuations over time, and the relative magnitude of those fluctuations can improve the ability to forecast future change and could have broad-reaching implications for forest ecology. Small mammals play crucial roles in many ecosystems as vectors of zoonotic diseases ([Ostfeld et al. 2006](#)), consumers and dispersers of seeds and fungi ([Stephens and Rowe 2020](#); [Boone et al. 2022](#)), regulators of insect pests ([Elkinton et al. 1996](#)), and serve as food resources for many avian and mammalian predators ([Boutin 1995](#); [Boonstra et al. 1998](#)). Additionally, due to their high abundance, small mammals can play a substantial role in the transfer of energy from plants to both predators and decomposers ([Krebs et al. 2019](#)). Therefore, any alteration to small mammal population or community dynamics through natural or anthropogenic disturbance could have cascading effects across the ecosystem.

Here, we used 30 yr of data (1994 to 2023) from a study at Bartlett Experimental Forest in the White Mountain National Forest in central New Hampshire, USA, which was established coincident with several silvicultural prescriptions. Our specific objective was to determine the relative roles that weather, forest structure, and pulsed food resources play on interannual fluctuations in small

mammal abundance. We utilized Bayesian N-mixture models to estimate the abundance of 9 species in response to a suite of environmental factors while accounting for imperfect detection. The mixed conifer-hardwood forests of New England, USA, provide an excellent system for investigating the effects of both annual variation in resource availability and habitat disturbance on small mammal populations. Pulses in resource availability are mainly driven by the presence of several common masting tree species. Masting species are generally defined as those that exhibit highly variable and regionally synchronized seed production, resulting in years of high seed production followed by 1 or more years of very limited seed production (Ostfeld and Keesing 2000; Koenig 2021). In this system, American Beech (*Fagus grandifolia*) and Red Maple (*Acer rubrum*) are the predominant masting species, both of which are a primary food resource for many small mammals (Moore et al. 2022). The assemblage of small mammal species within the Bartlett Experimental Forest is diverse, comprised of shrews (primarily insectivorous) and rodents with diverse diets (granivorous, herbivorous, fungivorous)

and overwintering strategies, allowing for the examination of population trends for species with varying ecologies.

Methods

Study site.

The Bartlett Experimental Forest (hereafter, Bartlett) is located within the White Mountain National Forest in north-central New Hampshire, USA (44°3'7.2"N, -71°17'25.1"W; Fig. 1a). The experimental forest was established in 1931 by the USDA Forest Service and expanded from an original 1,052 ha to 2,343 ha in 2005 (King et al. 2011). Previously, this area underwent substantial harvesting between 1887 and 1894 (Belcher 1980) and is currently dominated by mature secondary successional deciduous and coniferous forest types. Dominant tree species include American Beech, Sugar Maple (*Acer saccharum*), Red Maple, Yellow Birch (*Betula alleghaniensis*), Eastern Hemlock (*Tsuga canadensis*), Red Spruce (*Picea rubens*), and Balsam Fir (*Abies balsamea*; Ducey et al. 2023). The climate is humid

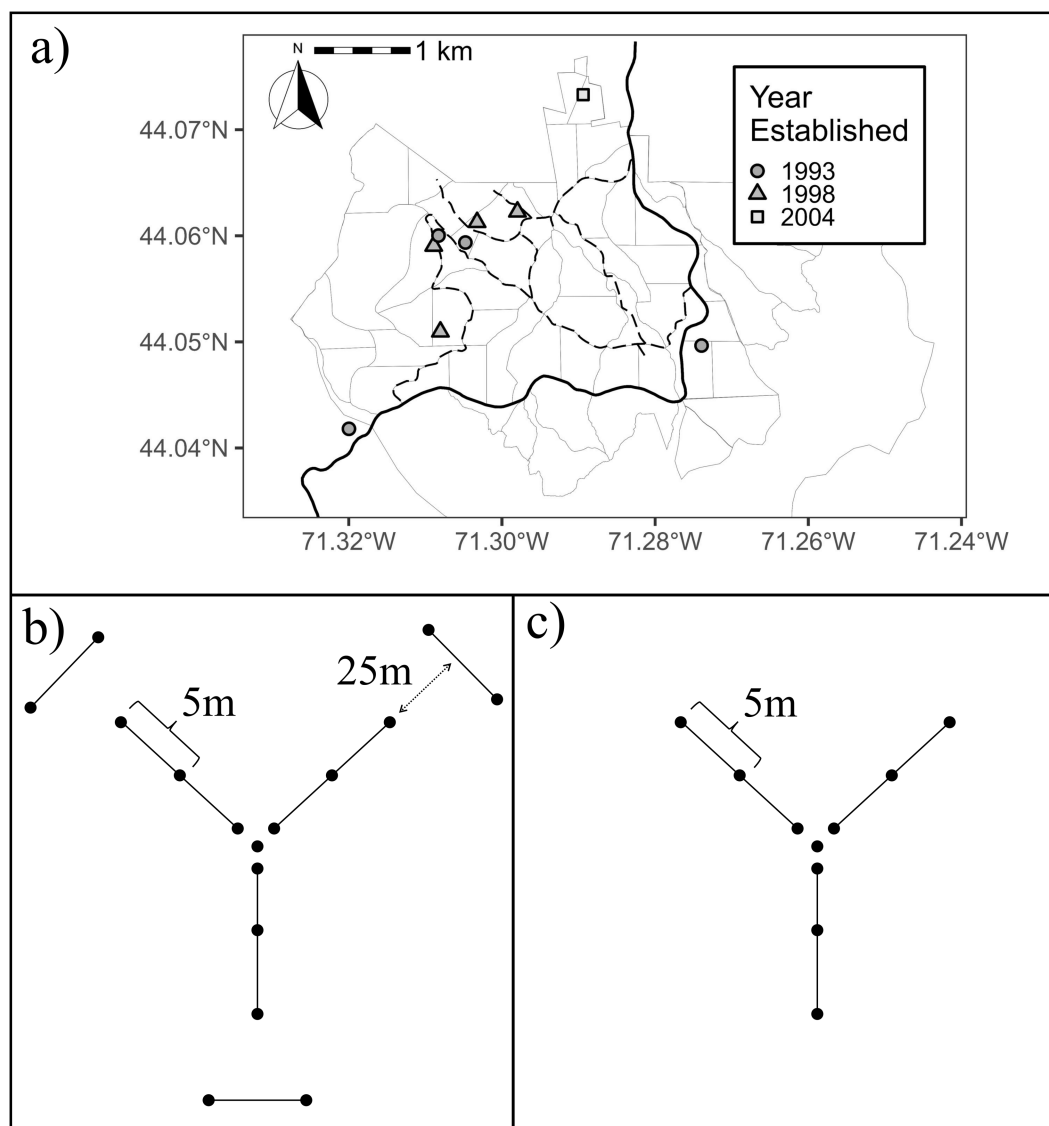


Fig. 1. a) Map of Bartlett Experimental Forest in central New Hampshire, USA, showing the distribution of sites and diagrams of pitfall trap layout at b) the original 4 sites with 16 total traps and c) the subsequently established sites with 10 total traps. In panel a), points represent sites established in 1993, triangles represent sites added in 1998, and squares represent sites added in 2004. The solid line represents the paved Bear Notch Road that bisects the study area, and the dashed lines represent gravel roads throughout the interior of the experimental forest. In panels b) and c), dots represent individual pitfall buckets, and lines represent drift fencing between buckets (distances not shown to scale).

continental with warm summers (highs reach into the low 30 °C) and cold winters (lows reach −5°C) with substantial snow (depths 150–180 cm; King et al. 2011).

Small mammal surveys.

Nine small mammal survey sites were established at Bartlett (4 in 1993, 4 in 1998, and 1 in 2004; Fig. 1a) coincident with different timber harvest prescriptions; all sites were monitored through 2023. The sites were established in predominantly hardwood stands, except for the site established in 2004, which was located within a conifer-dominated stand consisting primarily of White Pine (*Pinus strobus*). The unharvested control site was established in a mature hardwood stand. Prescriptions spanned even-aged (clearcuts, patch cuts, shelterwood) and uneven-aged (single-tree selection, group selection) management methods. Clearcuts were ca. 8.1 ha in size, patch cuts were ca. 2 ha in size, and group selection prescriptions resulted in 0.1–0.8 ha openings. Single-tree selection and shelterwood prescriptions were implemented to reduce residual basal area to 16 to 18 m² per hectare and 23 m² per hectare, respectively. One of the sites added in 1998 was included to examine small mammal response to natural disturbance, specifically a severe 100-yr ice storm that passed through the region causing widespread tree damage (Lorimer and White 2003).

At each site, small mammals were surveyed via removal sampling using an array of pitfall traps. The original 4 sites established in 1993 consisted of 16 trap stations. Traps were arranged 5 m apart in a Y-shaped array with 3 transects radiating out from a central point. Each transect had an additional 2 “remote” traps placed perpendicular to the main transect and at least 25 m away (Fig. 1b). All subsequent sites consisted of 10 traps arranged in the same Y-shaped array as the original sites but without the additional “remote” traps (Fig. 1c). Each pitfall trap (a 3-L bucket, 14.5 cm diameter by 18 cm tall) was buried until the lip of the bucket was level with the soil surface and filled part-way with water and a small amount of dish soap to act as a surfactant. Trapping was conducted 3 times per year over the summer (Jun to Sept) centered around the new moon. Each trap session consisted of 10 consecutive trap days. Traps were checked once per day and all captures were identified to species, labeled, and deposited in a freezer. Many specimens were prepared as vouchers and deposited in natural history collections. At the end of each trap session, the pitfalls were closed and fluid emptied to prevent incidental bycatch between trap sessions. At least 1 yr of preharvest trapping data were collected at 6 of the 7 treatment sites. All sampling procedures adhered to guidelines outlined by the American Society of Mammalogists (Sikes et al. 2016) and were approved by the University of New Hampshire Animal Care and Use Committee for years when operations were managed by UNH rather than the Forest Service (protocol 220603). The total number of trap nights across the entire 31-yr study ranged from 6,000 to 14,880 per site (96,720 total) with 25,109 individuals across 18 species (12 rodents and 6 shrews) captured to date.

Environmental variables.

Beech mast

American Beech mast is a high-value food resource for small mammals in this system (Stephens et al. 2019; Moore et al. 2022) and shows a large degree of interannual variability. American Beech masting is generally synchronized across regions (Piovesan and Adams 2001). We obtained long-term data on beech mast from the Hubbard Brook Experimental Forest (hereafter, Hubbard Brook), located approximately 35 km southwest of Bartlett (Fahey and Cleavitt 2021). Beech mast has recently been collected at Bartlett (2017 to 2022) and is highly correlated with that of Hubbard Brook

($r^2 = 0.98$; $P < 0.05$). We used the Hubbard Brook mast data to calculate the mean number of beech seeds per m² for each year (1993 to 2022). We excluded data from experimental site W1 in Hubbard Brook to avoid any influence of calcium supplementation experiments on mast intensity at that site. Because most beech seeds fall in autumn after trapping has ceased for the year, we used the mast from the preceding fall when modeling abundance in each summer.

Forest structure

We included herbaceous cover and relative stand density (RSD) because they capture changes in the understory and overstory structure, respectively, both of which can strongly change the habitat quality for small mammals. To assess the effects of forest regeneration, we used data on tree species and understory cover that had been collected every 2 to 4 yr in most treatment stands, with single-tree and control stands surveyed less frequently. Overstory trees were inventoried on a variable radius plot using a 2.3 m² per hectare prism sweep where the DBH and species were recorded for all “in” trees with a DBH ≥ 8.9 cm. Using a fixed area plot (radius = 2.27 m) at the center of each pitfall array, all woody stems greater than 0.5 m tall and with a DBH < 8.9 cm. were counted and binned into 1 of 4 size classes (< 1 cm, 1.3 to 3.6 cm, 3.8 to 6.1 cm, 6.4 to 8.6 cm). We combined data from these 2 sampling methods to calculate the Ducey–Knapp RSD index (Ducey and Knapp 2010) for each site. Additionally, understory herbaceous cover was measured using 2 circular milacre plots at each array, with 1 plot placed at the center of the array and the other randomly within the array. Within each plot, percent cover by species was estimated for all herbaceous plants as well as seedlings of woody species that were < 0.5 m tall. Due to the slow nature of forest regeneration, surveys were not performed every year. Missing data from years in which surveys were not conducted were imputed using a weighted moving average. Missing values after the final year of sampling were fixed at the last measured value.

Weather

Weather can impact small mammal populations directly through overwinter survival and indirectly through the availability of forage during the breeding season. To capture these drivers, we incorporated 3 different variables: summer precipitation; winter temperature; and winter snow depth. We obtained all weather data from a NOAA weather station in North Conway, NH (station ID: USC00275995; 44.0562° N, −71.1297° W). The station ranged from 11.4 to 14.0 km from the trapping arrays (mean distance: 12.6 km). Fine temporal scale weather data extending back to the start of the study are not available for Bartlett itself, therefore necessitating the use of the closest weather station with complete historical data.

For summer precipitation, we calculated the total cumulative amount of rainfall from 1 May to the first day of each trap period. We chose this cutoff because early May is typically when snow melt has finished and green-up has begun. For winter temperature and snow depth, we defined “winter” as the period from 1 November to 31 March of the following year. For each winter period, we calculated the deviation in mean daily minimum temperature from the long-term mean daily minimum temperature. To do this, we first calculated the overall mean daily minimum temperature across all years (1993 to 2023) and then calculated the daily deviation in minimum temperature from this long-term mean. We chose this metric rather than a simple mean minimum temperature because we were interested in examining how extreme weather events (i.e., abnormally warm or cold winters) impacted small mammals. For each winter period, we also calculated total number of days in which the accumulated snow depth was ≥ 20 cm. We chose this value as a cutoff

because previous studies have found that snow depths ≥ 20 cm offer substantial insulation to small mammals utilizing the subnivean space (Courtin et al. 1991; Reid et al. 2012). To confirm that snow depth at the weather station was representative of that at Bartlett, we extracted data from a set of National Ecological Observatory Network (NEON) snow stakes (National Ecological Observatory Network (NEON) 2023) established in 2016 and found the 2 datasets to be highly correlated (2016 to 2022, $r^2 = 0.90$; $P < 0.05$). When adding snow depth and winter temperature data to abundance models, the values from the winter preceding summer trapping were used.

Statistical analyses.

Using capture data from the small mammal surveys, we obtained yearly detection-corrected abundance estimates using hierarchical closed N-mixture models within a Bayesian framework. We were unable to obtain beech mast or weather data from 1992; therefore, we dropped the first year of trapping data (1993) from all analyses resulting in 30 yr of continuous trapping data. For each species, we assessed the performance of 4 different models: a Poisson model; a zero-inflated Poisson model; and both models with an added overdispersion random effect parameter in both the abundance and detection submodels. We evaluated the overdispersion random effect to account for any potential variation in the data not explained by the included covariates (Kery and Schaub 2012). For the Poisson and over-dispersed Poisson models, we modeled abundance at each site i during each year k and trap session m , $N_{i,k,m}$, as:

$$N_{i,k,m} \sim \text{Poisson}(\lambda_{i,k,m}),$$

where $\lambda_{i,k,m}$ denotes the expected abundance. For the zero-inflated Poisson and over-dispersed zero-inflated Poisson models, we modeled abundance as:

$$N_{i,k,m} \sim \text{Poisson}(\lambda_{i,k,m} * Z_k),$$

where Z_k represents a latent variable indicating whether the species was present or absent and was modeled as following a Bernoulli distribution:

$$Z_k \sim \text{Bernoulli}(\Psi_k).$$

We added a small constant, $1e^{-10}$, to the result of the Bernoulli distribution to prevent the value from resulting in zero and preventing model convergence. For both versions, we modeled covariate effects of mast availability, forest structure, and weather as:

$$\log(\lambda_{i,k,m}) = \alpha_{\text{site}} + \alpha_{\text{covous}} * X_{\text{covous}} + \log(\text{TrapNo}_i),$$

where α_{site} is a site-specific random intercept, α_{covous} is a conformable vector of covariate effects, X_{covous} represents the covariates included in the model, and TrapNo_i is an offset term to control for variable effort quantified as the number of traps per site i .

For the over-dispersed versions of the models we added a site, year, and trap session-level overdispersion random effect parameter, $\varepsilon_{m,k,i}$, to the abundance submodel. This parameter was modeled using a normal distribution with a mean of zero and a model-estimated variance.

The detection submodel accounted for imperfect detection and accommodated removal trapping. We assumed that detection probability, $n_{i,k,m,n}$, followed a binomial distribution:

$$n_{i,k,m,n} \sim \text{Binomial}(\rho_{i,k,m,n}, N_{i,k,m} - R_{i,k,m,n}),$$

where $\rho_{i,k,m,n}$ is the detection probability at site i in year k , trap session m , and trap day n . As described in Stephens et al. (2017), to account for removal of individuals, we subtracted the number of individuals captured the previous day from the total number of individuals in the population (i.e., abundance N), resulting in a post-removal population size R such that:

$$R_{i,k,m,n} = N_{i,k,m} - \text{sum}(y_{i,k,m,n-1}).$$

We modeled the effects of overnight temperature, overnight precipitation, and Julian date on detection probability as:

$$\text{logit}(\rho_{i,k,m,n}) = \beta_{\text{site}} + \beta_{\text{covous}} * X_{\text{covous}} + \log(\text{TrapNo}_i),$$

where β_{site} is a site-specific random intercept, β_{covous} is a conformable vector of covariate effects, X_{covous} represents the covariates included in the model, and TrapNo_i is an offset, as above. As with the abundance submodel, for the over-dispersed versions of the models we added a site, year, trap session, and trap day-level overdispersion random effect parameter, $\varepsilon_{i,k,m,n}$, to the abundance submodel.

We estimated all parameters in a Bayesian framework using Markov Chain Monte Carlo methods in R (R Core Team 2019) using the “R2jags” package (Su and Yajima 2021). All continuous covariates were scaled to facilitate effect size and magnitude comparisons and all covariates were checked for collinearity with a 0.8 correlation coefficient used as a cutoff. We considered covariates to be statistically significant when the 95% credible interval did not contain zero. We ran 3 chains of 500,000 iterations each in parallel. We discarded the first 200,000 iterations as burn-in and set the thinning rate to 30 to reduce model output file size, resulting in 10,000 retained samples from which we created posterior distributions for each parameter. We used noninformative priors for all parameters (see Supplementary Data SD1 for full model specification). We assessed model fit by examining the deviance information criterion (DIC) score as well as by conducting a posterior predictive check using a chi-squared deviance statistic and calculated Bayesian P-values on both simulated data from the model and the observed data (Kery and Royle 2020). We tested each model for each species and reported only results from the best-fitting model, which was the model with the lowest DIC and acceptable Bayesian P-values (i.e., ≥ 0.05 and ≤ 0.95 ; Kery and Royle 2020). Additionally, we assessed convergence for all parameters using R-hat statistics (all values < 1.1 ; Gelman and Hill 2006).

Results

Eighteen small mammal species (12 rodents and 6 shrews) were captured over the duration of the study (Supplementary Data SD1). Of these, 9 had a large enough sample size for analysis (Table 1; Fig. 2). The over-dispersed zero-inflated Poisson model performed best for 5 of the species: Northern Short-tailed Shrew (*Blarina brevicauda*); Southern Red-backed Vole (*Myodes gapperi*); Woodland Jumping Mouse (*Napaeozapus insignis*); Deer Mouse (*Peromyscus maniculatus*); and Masked Shrew (*Sorex cinereus*). The over-dispersed Poisson model performed best for 2 species: White-footed Mouse (*Peromyscus leucopus*) and Smoky Shrew (*Sorex fumeus*). The normal Poisson model performed best for 2 species: Meadow Vole (*Microtus pennsylvanicus*) and Pygmy Shrew (*Sorex hoyi*).

Detection probability.

For all species, overnight precipitation increased detection probability and had the strongest effect on detection (Fig. 3). For all but 2 species, northern short-tailed shrews and white-footed mice, warmer overnight temperatures also increased detection probability (Fig. 3). Julian date had a more variable effect on species detection, with 5 species increasing in detection probability later in the summer (masked shrews, smoky shrews, southern red-backed voles, woodland jumping mice, and deer mice), 2 declining in detection probability as summer progressed (northern short-tailed shrews and meadow voles), and 2 showing no change in detection probability over the summer (pygmy shrews and white-footed mice).

Table 1. Scientific name, common name, and sample size (n) of all small mammal species captured at Bartlett Experimental Forest, NH, over the duration of the study (1993 to 2023).

Scientific name	Common name	n
Sorex cinereus	Masked Shrew	9,282
Napaeozapus insignis	Woodland Jumping Mouse	4,917
Blarina brevicauda	Northern Short-tailed Shrew	2,913
Peromyscus leucopus	White-footed Mouse	2,722
Myodes gapperi	Southern Red-backed Vole	2,655
Peromyscus maniculatus	Deer Mouse	1,757
Sorex fumeus	Smoky Shrew	1,149
Sorex hoyi	Pygmy Shrew	509
Microtus pennsylvanicus	Meadow Vole	253
<i>Synaptomys cooperi</i>	Southern Bog-lemming	119
<i>Sorex dispar</i>	Long-tailed Shrew	46
<i>Zapus hudsonius</i>	Meadow Jumping Mouse	31
<i>Condylura cristata</i>	Star-nosed Mole	21
<i>Sorex palustris</i>	Water Shrew	18
<i>Microtus pinetorum</i>	Woodland Vole	12
<i>Tamias striatus</i>	Eastern Chipmunk	11
<i>Parascalops breweri</i>	Hairy-tailed Mole	9
<i>Microtus chrotorhinus</i>	Rock Vole	5
	Total	26,429

Bolded species are those for which we have modeled abundance and its drivers.

Abundance

We found that all 6 environmental covariates were correlated with abundance of at least 1 species. However, species responses were highly variable both within and among covariates with no 2 species exhibiting the same overall response. Below we reflect on the degree to which these relationships could be driving abundance patterns through their effects on survival and recruitment. Most rodents increased in abundance the summer following a high-mast year; the 1 exception was woodland jumping mice which declined in abundance following a high-mast year except for northern short-tailed shrews, which increased in abundance and exhibited a stronger positive response to beech mast than any of the rodents (Fig. 3).

Likewise, RSD had varying effects on species abundance. Only 1 rodent (woodland jumping mice) and 2 shrew species (northern short-tailed shrews and smoky shrews) increased in abundance in response to increased stand density. Two rodents (meadow voles and white-footed mice) decreased in abundance as stand density increased (Fig. 3). Smoky shrews had the strongest positive response to stand density and meadow voles the strongest negative response. The amount of herbaceous cover had a positive effect on 2 species (pygmy shrews and woodland jumping mice), whereas both deer mice and white-footed mice responded negatively to increased understory vegetation (Fig. 3).

For most species, summer precipitation had a positive or neutral effect on abundance. However, 2 species (smoky shrews and deer mice) decreased in abundance during rainy summers (Fig. 3). Most species declined in abundance following winters with deeper snowpack, except for meadow voles, which increased

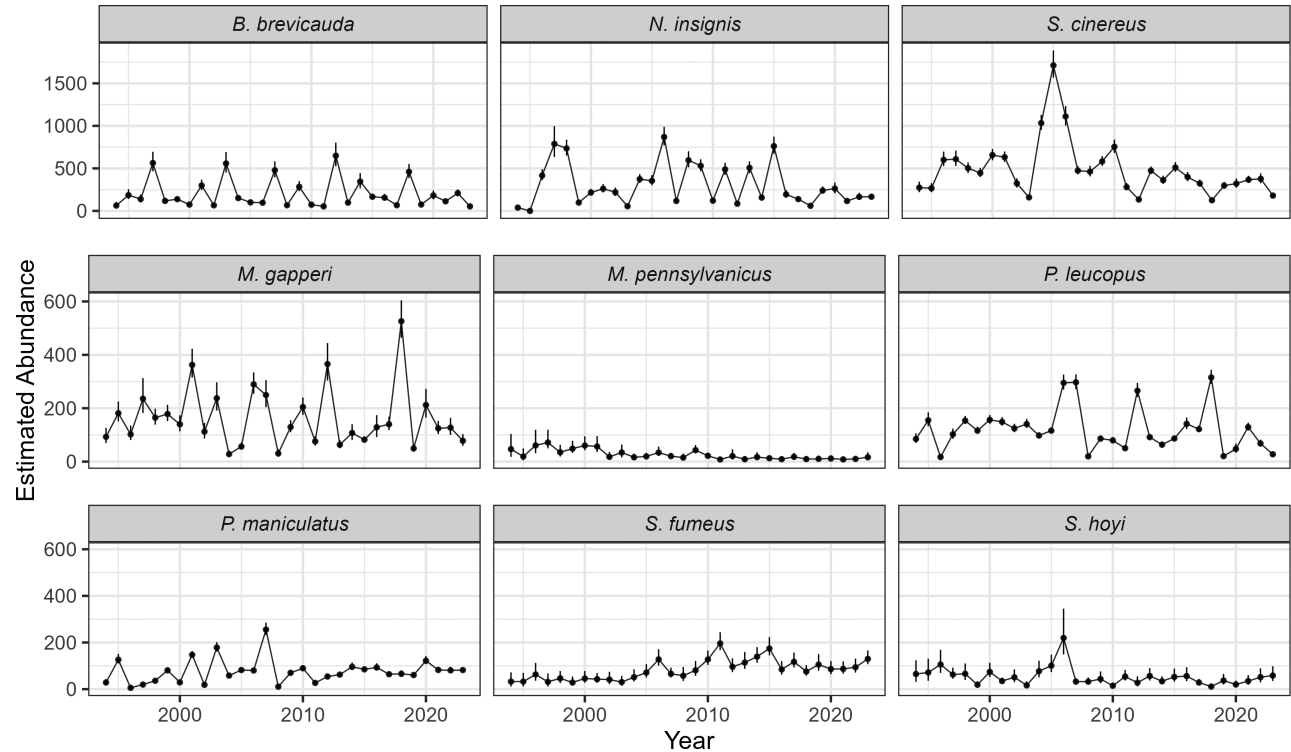


Fig. 2. Detection-corrected abundance estimates from 1994 to 2023 from N-mixture models for the 9 focal small mammal species from 1994 to 2023 at Bartlett Experimental Forest, NH. The x axis represents the study year, and the y axis represents the model-estimated average annual abundance (with 95% credible intervals) of each species. For clarity in seeing population fluctuations of species caught in lower abundances, the y axis scale in the lower 6 panels differs from that in the top 3 panels.

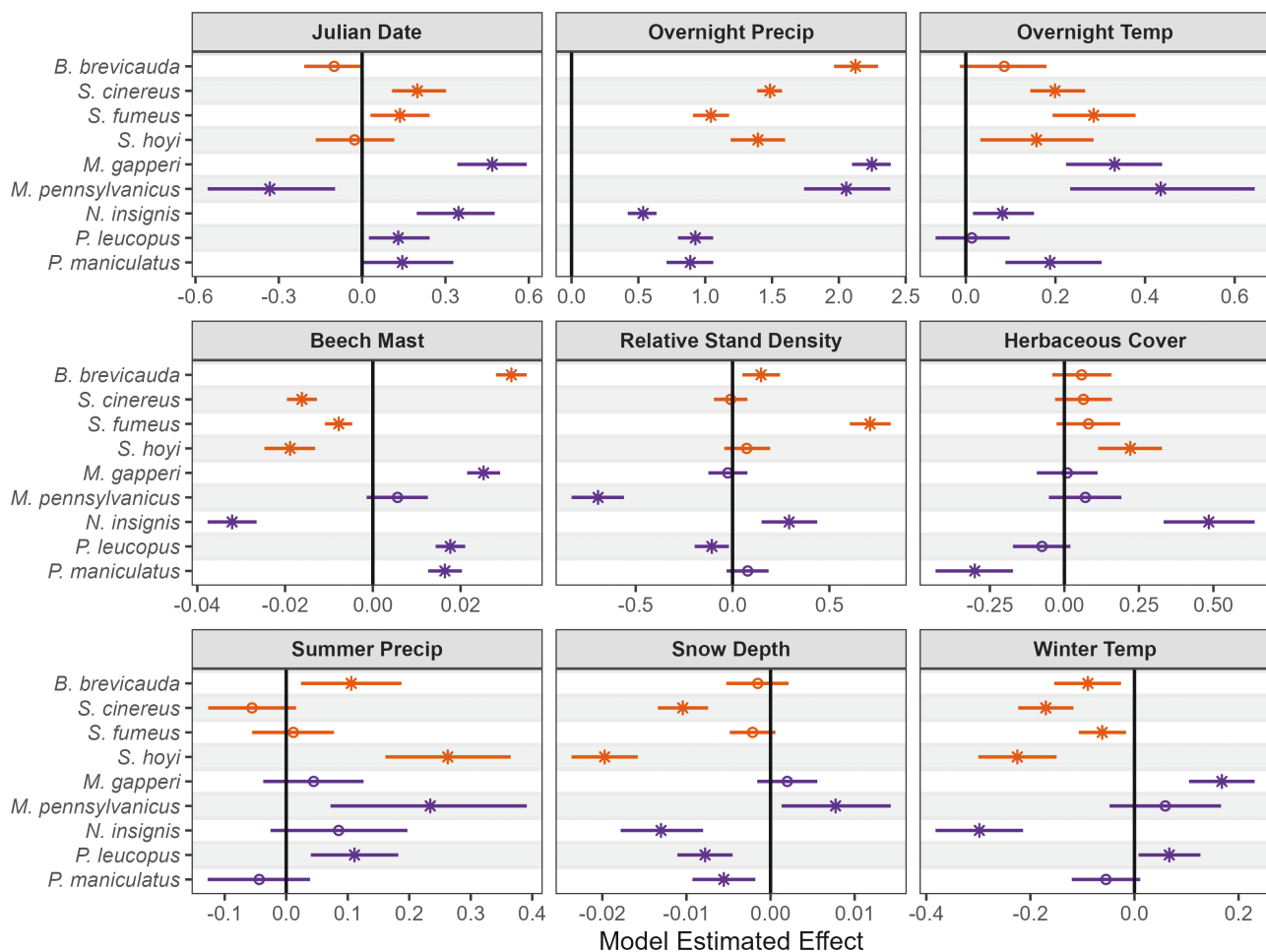


Fig. 3. Results of a Bayesian hierarchical model of abundance and detection probability for 9 small mammal species in Bartlett Experimental Forest, NH, from 1994 to 2023. Species were modeled individually and are ordered alphabetically, with shrew species listed before rodents. Detection results are indicated by (ρ). Points represent the mean model-estimated effect on abundance or detection probability and bars represent 95% credible intervals (CI). Solid asterisks represent parameters for which the 95% CI does not contain zero.

in abundance (Fig. 3). Increased winter temperature had a negative effect on the abundance of most species, although both red-backed voles and white-footed mice responded positively to milder winters (Fig. 3).

Discussion

Ecologists have long sought to understand what factors drive the distribution and abundance of species. Due to their ubiquity and short generation times, small mammals have become a model system for investigating the drivers of population fluctuations (Krebs and Myers 1974; Lindström et al. 2001; Krebs 2013). Answering this question and addressing the degree to which responses of species are synchronized requires long-term data to both capture the processes at work and the degree of variation that exists within those processes. Our study models abundance for 9 species, including both rodents and shrews, over a 30-yr period. Our results show that pulsed food resources, weather patterns, and forest structure all were correlated with abundance. However, these effects varied across species, and no single covariate seems to be driving the population dynamics of all species in this system. These findings underscore the complexity of response among species to disturbance—even for those with apparently similar ecologies—as well as the necessity of long-term monitoring to accurately tease apart differential responses from interannual variability in potential drivers.

Detection probability.

We found a great degree of conformity among the response of species to the detection probability covariates. Detection probability for all 9 species was positively associated with overnight precipitation, corroborating the results of many prior studies (Vickery and Rivest 1992; Otto and Roloff 2011; Maestri and Marinho 2014). One common explanation for this pattern is increased small mammal activity due to reduced predation risk associated with rainy nights (Vickery and Bider 1981). Warmer overnight temperatures had a similarly positive effect for most species except for northern short-tailed shrews and white-footed mice. Warmer nights could facilitate increased activity by reducing the physiological stress associated with foraging in cold conditions, especially for nocturnal small-bodied animals (Stokes et al. 2001). The response to Julian date was mixed. Detection probability could be expected to increase as the breeding season progresses due to increased abundances. This was true for most species; however, for northern short-tailed shrews and pygmy shrews detection did not change over the course of the summer and detection of meadow voles decreased later in the summer.

Beech mast.

In forested ecosystems, masting events provide a valuable, intermittent food source for many woodland species, including

rodents (Ostfeld et al. 1996; McCracken et al. 1999; Moore et al. 2022). In this study, we found that responses to increased American Beech mast mostly conformed to taxonomic lines. All but one rodent increased in abundance following a high-mast fall even though these rodents differ in their reliance on seeds. Past work has shown that Red-backed Vole diet is largely composed of fungi (Stephens and Rowe 2020), and among seeds, they prefer beech (Moore et al. 2022). *Peromyscus* also both prefer beech, but in years of low beech availability, they broaden their diets and select different food items, which may facilitate co-occurrence (Stephens et al. 2019). As such, the observed increase in abundance for these 3 species following a high-mast year is likely a result of either increased overwinter survival, increased reproductive activity or output, or a combination of these. Additionally, meadow voles were found to have a weak, positive response to beech mast, potentially due to their herbivorous diet predominantly comprised of grasses, sedges, and herbaceous plants (Reich 1981). Unlike the other mice, woodland jumping mice showed a sharp decrease in abundance following high-mast years. Although woodland jumping mice are known to consume beech seeds, they are overall less granivorous than these other rodents (Hamilton 1941; Whitaker 1962; Linzey and Linzey 1973; Orrock et al. 2003; Stephens et al. 2024) and are the only true hibernator in the system (Whitaker and Wrigley 1972). This difference in life history could prevent woodland jumping mice from taking advantage of pulsed food resources that occur in the fall just prior to or after individuals have entered hibernation (Stephens et al. 2024). Additionally, postmast increases in other rodent species could lead to greater competition for resources, resulting in reduced abundance of woodland jumping mice. Previous work has found that the abundance of woodland jumping mice is inversely correlated with the abundance of *Peromyscus* mice (Conrod and Reitsma 2015) and that the diet of woodland jumping mice changes in response to the abundance of deer mice (Orrock et al. 2003).

Whereas rodents generally increased in abundance following high-mast years, most shrews decreased in abundance. The 1 exception was the Northern Short-tailed Shrew, whose increase in abundance was somewhat surprising, especially since they exhibited the strongest positive response out of all species analyzed. Northern short-tailed shrews are large-bodied shrews (i.e., 18.6 g; Jones et al. 2009), comparable in size to the rodents in this system. Although they are generally considered to be insectivorous, they have a varied diet consisting of invertebrates, amphibians, small mammals, and vegetative matter, including beech seeds (Hamilton 1941). Both in the wild and in captivity, northern short-tailed shrews have been documented consuming, and even caching beech seeds (Babcock 1914; Hamilton 1941; Martin 1984). In addition to a direct increase in food availability from beech seeds, insectivorous species could benefit from a potential increase in woodland invertebrates during high-mast years. Previous work in the southern beech (*Nothofagus* spp.) forests of New Zealand, which exhibit similar masting patterns as American Beech forests, found that increased mast led to an increase in caterpillars and spiders, both of which were consumed by rodents (Kelly et al. 2008). The mechanism driving the reduced abundance of the smaller shrew species (Masked Shrew, Smoky Shrew, and Pygmy Shrew) in response to increased mast remains less clear. These species are not known to consume beech, and their much smaller size likely prevents them from breaking through the hard husk of beech seeds. As such, the negative response to beech mast that we observed could be due to indirect effects from competition or predation, or reflect an environmental variable correlated with masting events.

Forest structure.

Changes to forest composition and structure, through both timber harvest and natural disturbance can influence the abundance of small mammals (Davis et al. 2010; Urban and Swihart 2011; Earl et al. 2016). In this study, we examined 2 measures of forest structure: RSD and the amount of herbaceous understory cover, both of which were found to differentially affect species. Increases in both RSD and understory vegetation could reduce predation risk by providing greater cover (Perea et al. 2011; Sivy et al. 2011) and can modify microhabitat conditions by decreasing temperature, increasing soil moisture, and increasing leaf litter and woody debris, which may increase habitat suitability for northern short-tailed shrews, masked shrews, and woodland jumping mice which prefer cooler and more mesic conditions (Brannon 2002, 2005; Kaminski et al. 2007). The negative response of meadow voles to increased RSD is expected as this species is an open-habitat specialist that prefers wetter, tree-less areas (Stephens and Anderson 2014) and, as such, would be expected to decline in abundance as forest regeneration progressed and a closed canopy developed. The mechanism driving the negative response of white-footed mice to both RSD and understory vegetation as well as the negative response of deer mice to understory vegetation is less clear. Many small mammal species respond differently to different timber harvest prescriptions or intensities (Kellner and Swihart 2014). For example, past work has found highly variable responses of white-footed mice to changes in tree cover with increases (Fantz and Renken 2005), decreases (Schmid-Holmes and Drickamer 2001), and no change (Kaminski et al. 2007; Urban and Swihart 2011) in abundance following decreased canopy cover. Habitat generalists, such as *Peromyscus* mice, can also be abundant in edge habitats (Anderson et al. 2003), which could contribute to their mixed response to changes in forest structure.

Weather

Given their small body size and high surface-area to volume ratio, weather is critical to the thermoregulation of rodents and shrews and is also indirectly tied to resource availability. At northern latitudes, it is well understood that a stable subnivean environment is important for the overwinter survival of many small mammals (Marchand 1982; Scott et al. 2022). Our results unexpectedly suggest that an increase in snow cover is a negative driver of abundance. Most species (5 of 9) declined in abundance and only 1 species (Meadow Vole) increased in abundance following snow-heavy winters. Quantifying snowpack is challenging, particularly over long periods of time and using historic data, and it is possible that our measure does not adequately capture the subnivean conditions or may not do so at the appropriate spatial and temporal scale. Aside from how long snow cover persists and how deep it is, there are other aspects of snow (e.g., density, hardness, grain size and type) that affect its insulating properties and use by animals (Pruitt 2005). Accurate measures of these snow qualities cannot be readily calculated from data recorded at automated weather stations. Identifying the effects of snow on small mammals is also challenging because most studies (including this one) rely on trapping data in the spring or summer, once the bulk of the snow has melted and cannot directly capture how small mammals respond to acute variations in winter conditions.

Winter temperatures can also have a substantial effect on small mammal survival. Lower temperatures can lead to increased energy expenditures, potentially resulting in reduced overwinter survival (Wolff 1996). Intuitively, one might expect that warmer winters would be less physiologically stressful for small mammals and would therefore lead to an increase in overwinter survival. However, timing is important because repeated thaw-freeze cycles form

denser snow or ice, which is less insulating, and increased snowmelt during the postsubnival thawing period can be particularly challenging for some rodents due to the increased risk of nests being flooded and the thermal stress associated with having fewer dry refuges (Courtin et al. 1991). Woodland jumping mice, which are the only species in this system that hibernates (Whitaker and Wrigley 1972) had the strongest negative response to warmer winter temperatures, perhaps indicating that increased temperatures reduce the quality of the subnival habitat. We found that only 2 species, white-footed mice and red-backed voles, benefitted from warmer winters. White-footed mice are a more southerly distributed species (Pierce and Vogt 1993), and a previous study found warmer winters to have an immediate positive effect on their density suggesting increased survival (Lewellen and Vessey 1998). Southern red-backed voles are known to have generally poor overwinter survival in many systems (Boonstra and Krebs 2006). As such, warmer winters could result in increased overwinter survival of southern red-backed voles, leading to increased abundance in the summer.

Increased precipitation in the spring and early summer could have beneficial effects later in the summer through increased food availability (Williams et al. 2014), or detrimental effects such as flooding (Andersen et al. 2000; Elliott and Root 2006). We found the abundance of 5 species (Meadow Vole, Northern Short-tailed Shrew, Pygmy Shrew, White-footed Mouse, Woodland Jumping Mouse) to increase with increased spring and summer precipitation. This relationship has been noted previously for the Meadow Vole (Deitloff et al. 2010) and suggests that increased spring and summer rain lead to greater primary productivity of herbaceous plants, resulting in increased food availability. Additionally, previous studies have found a positive relationship between precipitation and the abundance of both white-footed mice (Merritt et al. 2004) and northern short-tailed shrews (Getz 1989). The exact mechanism of this positive association is unclear, although it could be due to increased availability of food such as invertebrates during wetter than average years (Williams et al. 2014). Both white-footed mice and northern short-tailed shrews are known to consume invertebrates (Hamilton 1941; Wolff et al. 1985), and an increase in invertebrate prey would also explain the observed positive effect of summer precipitation on pygmy shrews, which are also insectivores (Whitaker Jr. and Cudmore 1986). However, if this is the case, it is not clear why the same response was not seen in the other 2 *Sorex* species, which are also insectivorous.

In conclusion, small mammals play critical roles in many ecosystems as vectors for zoonotic diseases, dispersers for seeds and fungi, and a key food resource for many avian and mammalian predators. Our results underscore that small mammal species respond differently to pulsed food resources, forest structure, and weather patterns. Broadly speaking, we found that beech mast was positively associated with the abundance of granivorous and nongranivorous species, and that overnight temperature and precipitation were positively associated with increased detection probabilities of most species. However, responses to weather and forest structure were more varied. The differential responses that we observed might inform targeted management of certain species through timber harvest prescriptions as well as better predictions of ecosystem impacts under climate change or other stressors. For example, we found that white-footed mice and deer mice responded similarly to beech mast and forest regeneration. However, white-footed mice, one of the main vectors of Lyme disease (Ostfeld et al. 2006), responded positively to warmer winters and wetter summers, whereas deer mice, which are a less proficient vector of Lyme (Larson et al. 2018), did not. Climate change predictions for the northeastern US indicate that winters are likely to become warmer and summers wetter

(Tang and Beckage 2010), which could allow white-footed mice to outcompete and replace deer mice. This could, in turn, cause the spread of Lyme disease to areas where it is currently not prevalent, leading to significant ramifications for both human and wildlife health. Our results highlight the need for further investigation into the underlying drivers of population fluctuations in small mammals and how those dynamics scale-up to alter community dynamics and the ecosystem functions that they provision.

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1. Table of the total number of captures per species per year at Bartlett Experimental Forest, NH, from 1993 to 2023.

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Author contributions

M.Y. and C.C. developed and implemented the inventory and monitoring program. J.S.W., M.Y., and C.C. conducted and supervised the fieldwork. J.S.W. analyzed the data with support from R.J.M., M.J.D., and R.J.R. J.S.W. wrote the original draft of the manuscript. All authors reviewed and edited the manuscript. R.J.R. and M.Y. secured funding.

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Conflict of interest statement

None declared.

Data availability

Data and code to run all analyses are available upon reasonable request.

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