ASSESSING THE RESPONSE OF SMALL MAMMAL FUNCTIONAL GUILDS TO A SIMULATED PATHOGEN ATTACK IN A DECIDUOUS FOREST ECOSYSTEM

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ABSTRACT

Oak trees (*Quercus* species) are a foundation species that influence the population dynamics of other organisms by stabilizing ecosystem processes. Globally, oak-dominated forests have experienced widespread mortality due to the fungal pathogen, *Phytophthora ramorum*, which causes the disease Sudden Oak Death (SOD). I investigated the impact of a simulated pathogen attack such as SOD on the small mammal assemblage of an oak forest in Cornwall, New York. Specifically, I tested the hypothesis that specialist species are most impacted by the loss of foundation species and that they would decline in abundance because of changes in food and habitat resources.

In 2008, oaks were girdled to cause mortality and mimic the symptoms of SOD. Four treatments were established, with three replicates of each: 100% oaks girdled, 50% oaks girdled, 100% non-oaks girdled, and control. From 2008 to 2012, small mammals were live captured, individually marked, and released in each of the four treatments. In addition, environmental variables hypothesized to influence small mammal abundance were collected, including coarse woody debris, leaf fall, canopy openness, soil moisture and temperature.

Six small mammal species were captured, resulting in 5,135 total small mammal capture events. A total of 576 white-footed mice (*Peromyscus leucopus*) and 412 eastern chipmunks (*Tamias striatus*) were captured. These two species composed more than 97% of all animals captured. Small mammal species diversity, as measured by Shannon-Wiener diversity index, did not differ by treatment across years, but diversity was significantly lower in 2011 and 2012 across treatments. Decreased species diversity in the

fourth and fifth years after treatment suggests that the small mammal assemblage, specifically the resource specialist species, may be negatively impacted by landscape-level forest disturbances.

Full likelihood closed capture models indicated that abundance of the generalist white-footed mice and eastern chipmunks as well as their capture and recapture probabilities were not driven by the treatment conditions. Abundance did significantly vary by year for both white-footed mice and eastern chipmunks. White-footed mouse abundance was significantly higher in 2011and 2012 than all other years. Eastern chipmunk abundance was significantly higher in 2009 and 2012 and significantly lower in 2011. Northern short-tailed shrew (*Blarina brevicauda*) abundance significantly varied by year, but not treatment. Northern short-tailed shrew abundance was significantly higher in 2008 and 2009 compared to 2010-2012. Red-backed vole (*Clethrionomys gapperi*) abundance did not significantly differ by year, but it was significantly higher on control and 100% non-oak girdled plots compared to 50% oak girdled and 100% oak girdled plots. Meadow vole (*Microtus pennsylvanicus)* abundance varied significantly by year, but not by treatment, with abundance significantly higher in 2009 compared to all other years of the study.

Environmental conditions significantly varied by treatment, with coarse woody debris and soil moisture being greater in 100% oak and 50% oak girdled treatments. These habitat changes did not appear, however, to impact the generalist small mammal species. Relationships between these measured environmental variables and small

mammal abundance did not follow expected patterns, which may have been due to the relatively short duration of the study.

Based on my findings and due to their sensitivity to the altered environmental conditions, resource specialists such as northern short-tailed shrews and red-backed voles may be more appropriate biological indicators of ecosystem health following large-scale forest disturbance events. As the movement of pathogens globally accelerates, it will be increasingly important for ecologists to understand the bottom-up cascade of impacts related to the loss of foundation tree species.

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INTRODUCTION

Foundation species influence the population dynamics of other organisms by stabilizing ecosystem processes (Dayton 1972). Their abundance, architecture, and functional ecology control ecosystem dynamics (Ellison et al. 2005). Oak trees (*Quercus* spp.) in North America are a quintessential example of a foundation species as they are abundant in forest stands, provide habitat for other species, and produce energy-rich acorns that are a vital food resource for many bird and mammal species (Martin et al. 1961; Dickson 2004). As populations of other hardwood masting trees (e.g., American chestnut and American beech) decline, oak masts have become increasingly important to wildlife survival in the eastern United States (Healy et al. 1997; McShea et al. 2007; Ellison et al. 2010).

One emerging threat to the oak trees of North America and Europe is the fungal pathogen *Phytophthora ramorum,* which causes sudden oak death (SOD) (Garbelotto et al. 2001). First introduced to the western United States in 1995, SOD affects all oak species and over 100 additional plant species (Rizzo, Garbelotto, & Hansen 2005). Symptoms of SOD vary by host, ranging from localized twig infections to rapid defoliation and tree mortality within one year of infection (Rizzo et al. 2002; Rizzo, Garbelotto, & Hansen 2005; Nelson & Hudler 2007). If mortality is not immediate, SOD weakens plants, leaving them vulnerable to disturbances and attacks by opportunistic pathogens and pests including bark beetles, Ambrosia beetles, and other fungal pathogens (Rizzo & Garbelotto 2003). SOD is spread aboveground by asexual zoospores in wet environments or in the transport of soil or plant matter in the nursery trade (Nelson &

Hudler 2007). To date, SOD has infested natural forestland in 14 central and northern California coastal counties and one county in Oregon (Meentemeyer et al. 2008). Although its presence in wildlands is limited, by 2004, SOD had been confirmed in 176 nurseries in 21 states (Alexander 2012), leading to federal and state restrictions on interstate shipment of SOD-host plants from California nurseries (Alexander 2012). As of 2005, SOD was responsible for killing over 225,000 oak trees in the Big Sur eco-region of California (Meentemeyer et al. 2008). Property loss to California single family homes attributed to SOD is $135 million (Kovacs et al. 2011) and federal management and shipment restrictions have cost over $80 million (Frankel 2008). The wide breadth of host species, varying symptom severity, and ease of transmission make SOD a dynamic pathogen with the potential to permanently alter the deciduous forests of North America on a landscape scale (Sturrock et al. 2011).

Deciduous temperate forests such as those found throughout the eastern United States are typically regulated by one or a few foundation tree species including a variety of oak species (Ellison et al. 2005). When a pathogen such as SOD afflicts oak forests, it has the potential to significantly impact many fundamental ecosystem processes (Ellison et al. 2010). Little is known about the bottom-up cascade of effects resulting from foundation species-attacking pathogens, such as SOD. Previous research indicates that significant changes in forest composition can directly influence vertebrate population dynamics (Peles & Barrett 1996; Bowman et al. 2000; Fisher & Wilkinson 2005; Klenner & Sullivan 2009; White, McGill, & Lechowicz 2012). For example, models of the effect of SOD on oak-obligate bird populations indicate that areas with low oak diversity are

most susceptible to establishment of SOD. Bird population ranges in these areas of high susceptibility are smaller and more variable than pre-SOD estimates (Monahan & Koenig 2006). Although the impact of SOD on ticks and their vertebrate hosts as it relates to the prevalence of Lyme disease (Swei et al. 2011) has been investigated, the demographic response of small mammals to SOD has not been extensively studied.

Small mammals significantly contribute to vertebrate biodiversity and play a key role in forest ecosystems. Small mammals may help shape the succession of forests through seed and fungal consumption and dispersal (Tevis 1956; Gashwiler 1970; Maser, Trappe, & Nusbaum 1978, Price & Jenkins 1986), nutrient cycling, soil aeration (Sieg 1988), and as prey species for predators (Laudenslayer & Fargo 2002) such as bobcats (*Lynx rufus*), coyotes (*Canis latrans*), fishers (*Martes pennant*), great-horned (*Bubo virginianus*) and long-eared owls (*Asio otus*), and northern goshawks (*Accipiter gentilis;* Saunders 1988). Their integral role in the function of ecological processes, extensively studied natural history, and short generation time often make small mammals good indicator species for the health of an ecosystem (Landres, Verner, & Thomas 1988; Carey & Johnson 1995).

Small mammals respond to forest disturbances in a species-specific manner. In a meta-analysis of two of the most common types of forest disturbance: wildfire and timber management, Zwolak (2009) found deer mice (*Peromyscus maniculatus*) abundance increased while red-backed vole (*Clethrionomys gapperi*) abundance decreased following both wildfire and timber harvest disturbance. Additionally, clear cutting positively influenced deer mouse abundance for periods less than 10 years, while red-backed vole

abundance remained negatively influenced for up to 20 years (Zwolak 2009). Another study found that small mammal assemblage diversity was not affected by herbicide applications over a five-year period (Sullivan et al. 1998), while burning downed logs following clear-cutting reduced small mammal species diversity and abundance over a four-year period (Sullivan, Lautenschlager, & Wagner 1999).

The variation in small mammal species response to forest disturbance may be influenced by the habitat and food resource limitations of each species. All organisms can be classified along a specialization gradient, ranging from obligate habitat, food source, or environment specialist (e.g., woodland voles, *Microtus pinetorum*) to generalists, with acclimation to a wide range of conditions and food sources (e.g., white-footed mice, *P. leucopus*) (McPeek 1996). Generalist species obtain necessary resources from a variety of sources in a heterogeneous environment (Orrock et al. 2000), while specialist species have narrower habitat ranges and greater dietary restrictions (Aava 2001). Generalist species are typically more dominant compared to resource specialists, due to the generalist's broader niche breadth (Levins 1968). Within assemblages, species can be classified into functional guilds based on their habitat and food specialization. Differences in species dominance and space utilization among each guild require special consideration when analyzing the response of small mammal communities to environmental change. The variability in the small mammal species-specific response to disturbance is especially important due to their ecological role in forest systems.

Although many studies have addressed small mammal assemblage response to forest disturbance, less is known about how specific environmental changes mediated by

pathogen-related forest disturbance impact small mammal populations. In particular, the loss of foundation species due to a forest pathogen may substantially affect small mammal assemblages because small mammals rely on foundation tree species to provide structure and to regulate ecosystem processes. Small mammal species are sensitive to environmental change. The response of species abundance to altered habitat can be used to make predictions about the anticipated bottom-up cascade of effects due to the emergence of novel forest pathogens.

The main objective of my study was to investigate the demographic response of small mammal species to environmental changes associated with a simulated pathogen attack in deciduous forest ecosystems. I investigated changes in small mammal abundance and diversity as well as several environmental variables in an oak-dominated forest of upstate New York in which treatments have been applied to simulate the effects of SOD. I hypothesized that specialist species such as shrews and voles would decrease in abundance in response to the foundational species loss and that generalist species would increase in response to the decline in specialist abundance. I additionally predicted that leaf fall and coarse woody debris would be related to small mammal species diversity and abundances because they provide increased cover, foraging, and nesting habitats for small mammals and their invertebrate prey. Study of the impact of forest perturbations on small mammal populations is necessary to understand the impact of landscape alterations on these vital members of the ecological community.

RESEARCH DESIGN AND METHODS

Study Site – The study was conducted in the Hudson Highlands of New York at Black Rock Forest (41.45° N, 74.01° W), a consortium-run private forest preserve used for research and education. Located 1.6 km from Cornwall, New York, Black Rock Forest (BRF) is 15.5 km^2 of mixed deciduous forest, comprised of 67% oak and 33% non-oak trees (Schuster et al. 2008). The experimental site is 67,500 m^2 in a mature oak stand (≈120 yr old) on the north slope of Black Rock Mountain (400 m asl). BRF has been oak-dominated for over 10,000 years (Maenza-Gmelch 1997), and the canopy is dominated by red oak (*Q. rubra*) and chestnut oak (*Q. prinus*). The predominant non-oak species found on the experimental plots are red maple (*Acer rubrum*), black gum (*Nyssa sylvatica*), black birch (*Betula lenta*), and sugar maple (*A. saccharum*). The average aboveground biomass of all trees in Black Rock forest was 242,436 kg per hectare, of which, 196,497 kg per hectare were oak trees (81%).

Experimental Design – This study was part of a larger investigation analyzing many aspects of the forest and their response to the simulated pathogen attack on foundation tree species. Although this study manipulated the oak trees of BRF, Sudden Oak Death does affect non-oak trees as well, so this study was not necessarily an accurate simulation of SOD. All data were collected and catalogued by other collaborators in the BRF environmental database and were made available for analysis in conjunction with the data I collected. The experiment used a randomized block design consisting of three plots (replicates) of four treatments for a total of 12 plots, each of which was 75 x75 m

(0.5625 ha; Fig. 1). To reduce edge effects, plots were separated by a buffer strip of a minimum of 25 m (Fig. 2).

The treatments were no girdling (control), all non-oak trees girdled (100% non-oak), 50% of oaks girdled (50% oak), and all oaks girdled (100% oak). Beginning in June 2008, chainsaws were used to notch girdle the circumference of the trees at breast height, cutting 5 cm into the phloem and cambium to mimic a pathogen attack, such as SOD. Tree girdling effectively caused tree mortality. In the 100% oak-girdled plots, all oak species of all sizes were girdled and in 50% oak-girdled plots, every other oak tree within the treatment area was systematically selected for girdling. Some trees, particularly non-oaks, survived the initial girdling treatment, and therefore re-girdling was performed as needed in 2010 and 2011.

Small Mammal Trapping – Animals were collected following a Columbia University Institutional Animal Care and Use Protocol (# 2012-029). Trapping sessions were conducted for 10 days per month in July-September 2008, May-September 2009, May-September 2010, May-August 2011, and May-July 2012. Twenty collapsible Sherman live traps (ten of each size; 7.5 x 7.5 x 25 cm, model: LFG, 10.2 x 11.4 x 38.1 cm, model: XLF15, H. B. Sherman Traps, Inc., Tallahassee, FL) were arranged in two concentric circles on each plot. The inner circle was 10 m from the center of the plot, while the outer circle was 10 m from the inner circle (Fig. 2). The trapping webs were positioned at the center of each plot, resulting in approximately 18 m of open space between the trapping web and the edge of the plot. This space combined with the minimum buffer strip of 25 m resulted in at least 60 m between each trapping web (Fig.

2), larger than the majority of home ranges of the small mammal species sampled (Newman 2010). Each trap was baited with crushed oats and ground peanut hearts as well as cotton balls or synthetic batting for nesting material. Trapping sessions were organized by replicate plot and each replicate was trapped sequentially for 3 trap nights per month. Traps were checked twice daily, after sunrise and in the afternoon. For analysis purposes, individuals captured during both the morning and afternoon sessions of the same day were only counted once for that day. Trapped individuals were processed at the site of capture. Animals were marked with a metal ear tag (model #1005-1, National Band and Tag Company, Newport, RI) in each ear. Species with small ears (e.g. shrews) were marked with a unique pattern cut into their fur. Individuals were categorized by species. Sex, mass, weather, time, and location of capture were recorded for every individual trapped. Individuals were weighed using a 300 g spring scale (model# 40300, Pesola, Baar, Switzerland). Following marking and recording, individuals were released at the site of capture.

Demographic Analysis – A full likelihood approach (Otis et al. 1978) in Program MARK version 7.1 (Ft. Collins, CO; White & Burnham 1999) was used to obtain capture ($\hat{p}$) and recapture ($\hat{c}$) probabilities and estimated annual abundance ($\widehat{N}$) of white-footed mice and eastern chipmunks (*Tamias striatus*), the two most encountered species in the study, for each treatment, in each year. A full likelihood approach was chosen because it includes *N* as a real, rather than derived, parameter in the likelihood (Otis et al. 1978). The full likelihood model assumes: (1) the population is closed, (2) marks are not lost or overlooked, and (3) all animals have an equal opportunity to be captured. The variables

$\hat{p}$, $\hat{c}$, and $\widehat{N}$ were calculated for individuals from the same treatment type for each of the five years of the study. A one-way ANOVA was used to investigate differences in $\widehat{N}$ estimates over time. Time was analyzed within each year, but not across years due to the low interannual survival of the study species. Minimum number alive (MNA; Krebs 1966) method of population estimation was used to estimate abundance of rare species with low capture frequencies. It was also used when white-footed mouse and eastern chipmunk capture frequencies were too low to estimate all model parameters using Program MARK. The sex ratio of white-footed mice and eastern chipmunks was analyzed using Pearson's chi-squared test (X^2; Pearson 1900) to identify significant differences among this categorical variable.

I used Akaike's Information Criteria (AIC; Akaike 1973) to objectively rank each model based on fit. To correct for small sample sizes, a corrected AIC value (AIC_c; Hurvich & Tsai 1989) was computed for each model. I used an information-theoretic philosophy of model selection (Burnham & Anderson 2002) throughout the analysis. To account for model selection uncertainty, I model-averaged $\hat{p}$ and $\hat{c}$ for each species (Burnham & Anderson 2002). Only models with $AIC_c > 0.100$ model weight were included in modeling averaging.

The abundance of each of the six captured species was included to analyze species diversity for each treatment and year using the Shannon-Wiener diversity index (Shannon 1948):

$$H' = - \sum_i^S p_i \ln (p_i)$$

The variable $p_i = \frac{n_i}{N}$; n_i is the abundance of the *i*th species; and N is the total abundance. An ANOVA identified if differences existed in species diversity among treatments and years.

Environmental Data Collection – Beginning on June 21, 2008, data loggers (CR10X, Campbell Scientific, Logan, UT) placed on the east and west corners of each plot recorded soil temperature (°C), soil moisture (volumetric water content, θ), and air temperature (°C). Leaf fall was collected in plastic baskets (0.36 m^2 rectangular baskets from 2008-2010 and 0.28 m^2 round baskets from 2011-2012) placed on the four corners of every plot and biomass (g) was measured at least once, but sometimes twice per year. Coarse woody debris (CWD) data were collected from two 4 m transects set-up from east to west on each of the 12 plots in 2010 and 2012. All pieces of dead wood greater than 7.5 cm in diameter were measured and recorded. Most pieces fit the "frustum of a cone" shape and therefore, three diameter measurements were taken equidistant apart on each piece. Additionally length was obtained and these measurements were used to calculate volume. Decay class, ranging from 1 (newly dead) to 5 (essentially soil), and species were also determined for each piece of CWD. Canopy openness was measured using hemispherical canopy photographs taken with a fish eye lens at the four corners of each plot, twice per year (leaf off and leaf on). Photographs were taken with a Nikon Coolpix camera (2008-2010 Nikon Coolpix 990; 2011-present Nikon Coolpix 4500) on a tripod, leveled at 1 ± 0.25 m above the ground and pointed to magnetic north. Photographs were analyzed using the program Sidelook version 1.1 (Nobis & Hunziker 2005) to objectively differentiate between areas consisting of sky and canopy cover. Images were analyzed

with Gap Light Analyzer version 2 (GLA, Frazer, Canham, & Lertzman 1999), which calculated percent of open sky and leaf area index of the canopy overstory. To measure ground vegetation cover, ten $1m^2$ subplots, arranged in two rows of five, were established in the center of each of the 12 plots in August 2010 (Palmer et al., unpublished data). Percent ground cover was determined by trained observers who visually estimated the percentage of vascular plant cover on a scale of 1 to 100%. Plants were identified to genus and species when known and classified as woody or herbaceous (Palmer et al., unpublished data).

I used total precipitation (mm) from the winter and spring seasons prior to small mammal trapping each year as an approximation of aboveground net primary productivity (ANPP). Precipitation was collected from rain gauges at the Open Lowland Station (41.25° N, 74.10° W) in BRF. The positive relationship between ANPP and precipitation has been well documented (Rosenzweig 1968; Walter 1971; Sala et al. 1988). I used precipitation from the prior seasons because small mammal populations respond to winter precipitation with a three- month lag time (Bradley et al. 2006). Oak mast was collected annually from mid-September to early October of each year. Sampling was conducted weekly at 15 locations in BRF with predetermined transects (Brady 1994), and acorn mast density was quantified using traditional methods (Eckert, Marquis, & Roach 1976). Samples were extrapolated to determine the total annual acorn crop per hectare in BRF.

Environmental Data Analysis – Soil temperature, soil moisture, air temperature, leaf fall, ground vegetation cover, coarse woody debris, and canopy openness

measurements of each treatment were calculated for each year in which measurements were collected. To avoid pseudoreplication, these measurements were averaged for each of the 12 plots. Annual acorn mast data were included as an approximation of food availability.

Species and Environmental Relationships – Annual estimated species abundance was compared to annual mean values of each environmental variable using Pearson product-moment correlation coefficient (Pearson 1895) in SPSS version 21 (SPSS IBM., New York, NY). Pearson's correlation coefficient (*r*) provides a measurement between -1 and 1 and represents the linear correlation or dependence between two variables. Pearson's *r* was used to identify potentially strong relationships between small mammal abundance and environmental variables. Strong correlations were used to identify key environmental variables to include as covariates in population modeling.

Canonical correspondence analysis (CCA) was used to investigate the effect of stand-level oak mortality on the small mammal species assemblage of BRF. By combining mean annual soil temperature, soil moisture, air temperature, leaf fall, ground vegetation cover, coarse woody debris and canopy openness measurements with estimated annual small mammal species abundance measurements. CCA allowed for an examination of the influence of the environmental conditions and treatment on species abundances.

Direct gradient analysis in CCA relies on *a priori* environmental conditions that have been hypothesized to influence species distribution (ter Braak 1995). Three separate direct gradient analysis CCAs were conducted in CANOCO version 4.5 (Wageningen,

Netherlands), one for each phase of the study: beginning (2008-2009), middle (2010-2011), and end (2012). The study was divided into these three phases because changes in environmental variables and small mammal species responses likely would occur over longer-than-annual time scales and because low sample sizes for both environmental variables and small mammal abundance estimates.

Due to their rare encounter frequency, resource specialists were condensed into family groups (voles and shrews) because rare species may skew the results of the CCA (ter Braak 1995). To improve output interpretability, rare species were downweighted to 10% of the weight of the two most common species captured (white-footed mice and eastern chipmunks). Biplots were scaled to better examine the species relationships and the canonical relationships were analyzed for statistical significance using a Monte-Carlo permutation test (9,999 permutations). Joint biplots were created for each phase to evaluate any possible associations between species data and environmental and treatment variables.

Statistical Analysis – Two-way analysis of variance was used to test the environmental variables for significant differences in treatment and year (ANOVA; Fit model, JMP version 10.0.0, SAS Institute, Inc. 2012). Assumptions of independence, normality, and homoscedasticity of residuals were checked (Goodness of Fit, JMP version 10.0.0, SAS Institute, Inc. 2012), and any variables that did not conform to the assumptions were analyzed using the Wilcoxon rank-sum non-parametric test (Wilcoxon 1945). An alpha value of 0.05 was used to determine the statistical significance of all

tests. All significantly different results were analyzed using Tukey's Honestly Significant Difference (HSD) post-hoc test to identify the source of variation (Hsu 1996).

RESULTS

The randomized block design of this study was tested to identify significant differences among replicates. Due to the proximity of neighboring blocks and lack of statistical significance ($P > 0.050$), all analyses were therefore conducted at the treatment-level, rather than the plot-level. Low samples sizes prevented analysis of treatment*year interactions of many variables. These variables were analyzed using a one-way ANOVA to identify significant differences among treatments and years.

Demographic Analysis – Six species were captured over 14,960 trap nights of this experiment, resulting in 5,135 total small mammal capture events. Combined full likelihood closed capture models and MNA estimated abundance of white-footed mice as 301 on the control, 212 on 100% oak-girdled, 222 on 50% oak-girdled, and 225 on 100% non-oak-girdled treatments over the five years of the study (Table 1a). Like white-footed mice, eastern chipmunk estimated abundance was obtained from both MNA and full likelihood closed capture models. 370 eastern chipmunks were estimated on the control, while 247 on 100% oak-girdled, 243 on 50% oak-girdled plots, and 243 eastern chipmunks on 100% non-oak-girdled treatments (Table 1b). Other species captured included 6 individual meadow voles (*Microtus pennsylvanicus)*, 12 individual pine voles (*Microtus pinetorum)*, 28 individual red-backed voles, 66 individual northern short-tailed shrews (*Blarina brevicauda),* and 5 individual unidentifiable Soricids (Table 1c). Due to the low capture and recapture frequencies of the shrew and vole species, only white-

footed mice and eastern chipmunk capture and recapture probabilities and abundance estimates were calculated using full likelihood closed capture models.

AIC_c weighting of full likelihood closed capture models indicated that eastern chipmunk and white-footed mouse abundance was not influenced by the treatment conditions (Appendix 1a, 1b). A one-way ANOVA determined that white-footed mouse ($P < 0.001$) and eastern chipmunk ($P < 0.001$) abundance significantly varied by year (Fig. 3). White-footed mice were significantly more abundant in 2011 and 2012 than all other years. Similarly, eastern chipmunks were more abundant in 2009 and 2012, but were significantly lower in 2011. Approximately 30% of marked white-footed mice and 12 % of eastern chipmunks were captured on more than one experimental treatment type. These individuals had to be removed from the mark-recapture analysis because their movements violated the assumptions of a closed population and confounded any demographic response to the treatment conditions. The majority of the white-footed mouse top ranked models included time and treatment invariant $\hat{p}$ while recapture probabilities varied between constant and time-variant (Appendix 1a). White-footed mouse abundance estimates were only treatment-variant in 2012 (Appendix 1a). Fewer models were available for analysis of eastern chipmunks due to low sample sizes in 2010 and 2011. The majority of eastern chipmunk top models included time and treatment invariant $\hat{p}$ and $\hat{c}$ (Appendix 1b). The abundance parameter of eastern chipmunk top models was treatment-variant and constant (Appendix 1b).

In 2011, male white-footed mice were significantly more abundant than females (130 males, 80 females; $X^2 = 10.963$, $df = 1$, $P < 0.001$), while no other years showed a

significant difference in sex ratios. Similarly, percentage of male white-footed mice was significantly higher than females on 50% oak (57 males, 35 females; $X^2 = 5.312$, $df = 1$, $P = 0.021$) and 100% non-oak (79 males, 52 females; $X^2 = 5.605$, $df = 1$, $P = 0.018$) girdled plots, while control and 100% oak girdled plots did not demonstrate a significant difference in sex of captured white-footed mice. The sex ratio of eastern chipmunks did not significantly differ by treatment or year.

White-footed mouse mass did not significantly differ by sex ($P = 0.644$) or by treatment ($P = 0.531$), but it did significantly differ by year ($P < 0.001$). A one-way ANOVA indicated that white-footed mouse mass was significantly higher in 2011 (+17.524 %) than 2010. Individual eastern chipmunk mass did not significantly vary by sex ($P = 0.104$); however, mass significantly differed by treatment ($P = 0.016$) and year ($P < 0.001$). Average eastern chipmunk mass was significantly lower (-10.010%) on 100% oak girdled plots compared to the control plots and was significantly lower in 2010 (-15.600%) and 2011 (-17.090%) compared to all other years.

Northern short-tailed shrew MNA abundance significantly varied by year ($P < 0.001$), but not treatment ($P = 0.799$). Northern short-tailed shrew abundance was significantly higher in 2008 and 2009 compared to 2010-2012. The MNA abundance of the unidentified Soricids did not significantly vary by year ($P = 0.102$) or treatment ($P = 0.426$). Red-backed vole MNA abundance did not significantly vary by year ($P = 0.060$). Red-backed vole abundance was significantly higher on control and 100% non-oak girdled plots compared to 50% oak girdled and 100% oak girdled plots ($P = 0.040$). Meadow vole MNA abundance varied significantly by year ($P < 0.001$), but not by

treatment (P = 0.426). Meadow vole abundance was significantly higher in 2009 compared to all other years of the study. Lastly, pine vole MNA abundance estimates did not significantly vary by treatment (P = 0.054) or year (P = 0.407). Shannon-Wiener species diversity significantly varied by year (P = 0.021). Diversity was significantly greater in 2009 ($e^{H'}$ = 2.999 species) and significantly lower in 2011($e^{H'}$ = 2.037 species) and 2012 ($e^{H'}$ = 2.026 species) compared to all other years. Species diversity did not vary by treatment (P = 0.740).

Environmental Data Analysis – All but three environmental variables significantly differed by treatment (Table 2): air temperature (P = 0.829), canopy openness (P = 0.233) and leaf fall (P = 0.617). Soil moisture and coarse woody debris were significantly higher on 100% oak girdled and 50% oak girdled treatments than the control and 100% non-oak girdled treatments. Soil temperature was 22% greater on 100% non-oak girdled plots than 100% oak girdled treatments. Percent ground vegetation cover was significantly higher on the 100% oak girdled treatment compared to all other treatments.

Acorn mast was significantly higher in 2010 (P < 0.001) compared to all other years (Table 2, Fig. 4). All environmental variables except precipitation significantly varied by year (Table 2). No obvious linear trends were present in the annual changes to the environmental variables collected. Canopy openness (P = 0.002) and air temperature (P < 0.001) were significantly higher in 2010 than all other years. Soil temperature was significantly different each year (P = 0.004). Coarse woody debris and soil temperature were significantly highest in 2012. Significant year*treatment interactions were observed

in soil temperature ($P < 0.001$) and soil moisture ($P < 0.001$). Neither spring ($P = 0.670$) nor winter ($P = 0.190$) prior precipitation varied by year (Table 2).

Species and Environmental Relationships – Pearson's correlation coefficient identified statistically significant relationships between many of the environmental variables analyzed in this study (Table 3). Soil temperature and soil moisture were negatively correlated ($r^2 = -0.554$, $P = 0.011$, $N = 20$). Leaf fall was significantly correlated with four other variables, making it the most correlated variable of the study. Positive correlations with leaf fall included air temperature ($r^2 = 0.770$, $P < 0.001$, $N = 16$) and percent canopy openness ($r^2 = 0.677$, $P = 0.016$, $N = 12$). Percent ground vegetation cover had a strong negative correlation with leaf fall ($r^2 = -0.991$, $P = 0.009$, $N = 4$). Additionally, soil moisture was negatively correlated with leaf fall ($r^2 = -0.592$, $P = 0.016$, $N = 16$). Air temperature was positively correlated with volume of coarse woody debris ($r^2 = 0.746$, $P = 0.033$, $N = 8$) and percent canopy openness ($r^2 = 0.826$, $P = 0.001$, $N = 12$). White-footed mice and eastern chipmunk estimated abundance showed no significant correlation (positive or negative) with any of the measured environmental variables.

CCA identified key habitat associations among small mammal species and specific environmental and treatment variables. The CCA examining the early years of the study (2008-2009) explained 99.8% (axis 1: 93.7%, axis 2: 6.1%) of the species/habitat associations (Fig. 5a). The CCA did not detect a significant influence ($F = 12.01$, $P = 0.127$) of environmental covariates on small mammal abundance.

Although not statistically significant, biologically relevant associations between habitat variables and treatment plots were identified. The horizontal axis of the early years of the study displayed an association between canopy openness and 100% oak girdled plots (Fig. 5a). Likewise, the vertical axis demonstrated a strong positive association between 50% oak girdled plots and shrew abundance. This association with intermediately disturbed treatment plots and resource specialist species can also be seen with voles, which were positioned between the strongly associated 50% oak girdled and 100% non-oak girdled treatment plots.

The CCA examining the middle years of the study (2010-2011) explained 100% (axis 1: 96.2%, axis 2: 3.85%) of the species relationships (Fig. 5b). I did not detect a significant influence ($F = 32.55$, $P = 0.168$) of environmental covariates on small mammal abundance in 2010-2011. Surprisingly in 2010-2011, a strong positive association between canopy openness and 100% non-oak girdled plots was observed; shifting from its association with 100% oak girdled plots in 2008-2009. The vertical axis in 2010-2011 demonstrated a strong association between voles and 100% non-oak girdled plots, similar to the association seen in 2008-2009. A strong inverse relationship, based on orientations in opposite quadrants was observed between air temperature and soil moisture. Shrews were no longer associated with intermediately disturbed treatment plots. The 50% oak girdled treatment was no longer associated with the 100% non-oak girdled treatment, but rather had shifted to a strong association with the 100% oak girdled treatment.

In the final year of the study, 2012, the CCA explained 100% (axis 1: 80%, axis 2: 20%) of the species relationships (Fig. 5c). Like the other CCAs, no statistically significant association was detected between species abundance and the environmental variables ($F = 2.66$, $P = 0.087$), although biologically relevant associations were observed. An inverse relationship between the control treatment and all other environmental and treatment variables was detected on the horizontal axis of the 2012 CCA. In 2012, soil temperature was no longer inversely related to soil moisture, rather they were found in the same quadrant.

DISCUSSION

Small Mammal Response to Disturbance – This study shows that generalist species appear to quickly acclimate to severely altered environmental conditions. This conclusion is consistent with other studies that indicate that the abundance estimates of eastern chipmunks and several species of mice in the genus *Peromyscus* remain the same or increase in response to extensive habitat manipulation (Dueser & Shugart 1978; Morrison & Anthony 1988; Lehmkuhl et al. 1999; Sullivan, Lautenschlager, & Wagner 1999).

The omnivorous diet of generalist species may improve their ability to acclimate to altered environmental conditions. The diet of mice in the genus *Peromyscus* consists of four out of five major food categories available to small mammals, including fungi and lichens, seeds, herbaceous material, and invertebrates (Gunther, Horn, & Babb 1983). Similarly, eastern chipmunks consume herbaceous material, invertebrates, and fungi (Wrazen & Svedsen 1978). The generalist diets of white-footed mice and eastern

chipmunks may have influenced their ability to acclimate to the treatment conditions of this study (Newman 2010).

Acorns represent the majority of the winter larder collected and stored by small mammals (Goodrum, Reid, & Boyd 1971; Gashwiler 1979). Acorn crop yields in autumn significantly impact small mammal populations the following summer (Wolff 1996). White-footed mice and eastern chipmunk summer population densities generally peak following peak acorn production the previous summer (Ostfeld, Jones, & Wolff 1996). Although capture and recapture probabilities did not respond to the increased acorn crop in 2010, white-footed mouse mass was significantly higher on control plots in 2011. White-footed mice appeared to be more responsive to increased acorn availability compared to eastern chipmunks in BRF. Chipmunk mass was significantly lower in 2011 compared to all other years. Shifts in numerical dominance similar to this one from eastern chipmunks to white-footed mice within this system have been documented in other small mammal communities (Fonseca & Robinson 1990). This shift may suggest that white-footed mouse abundance negatively affected the carrying capacity of other small mammal species in BRF. While both species are generalists, the dramatic increase in white-footed mouse abundance indicates a stronger association between white-footed mice and acorn mast. Additionally, I hypothesize that the shift in numerical dominance was due to competition for space use, rather than direct competition for food resources between white-footed mice and eastern chipmunks. The ability of generalist small mammals to alter their diet composition based on changes in food availability caused by

forest disturbance may increase the likelihood of these species persisting in disturbed forest environments.

Although the treatments affected environmental variables, eastern chipmunks and white-footed mice abundances were not influenced by the treatment conditions. This was surprising because multiple generalist species have exhibited a positive response to forest disturbance events including forest thinning and wildfire (Tester 1965; Ahlgren 1966; Krefting & Ahlgren 1974; Bock & Bock 1983; Martell 1984; Carey 2000; Kyle & Block 2000; Wilson & Carey 2000; Carey & Wilson 2001; Sullivan & Lindgren 2001; Suzuki & Hayes 2003). This lack of generalist small mammal abundance response to the experimental treatment conditions may be due to the short duration of this study following manipulation. Also, because the trees were left standing following girdling, the cumulative effects of changes to multiple environmental variables did not occur on the same timescale. These inconsistent changes may have dampened or delayed the small mammal population responses to environmental change.

The results of this study did not support the hypothesis that specialist species (e.g., shrews, voles) would decrease in abundance on oak-girdled plots. Instead, specialist small mammals decreased in abundance over time and across all treatments, including the control plots. This experiment-wide decrease in specialist species abundance may be the result of cyclic population fluctuations common among small mammal species. These fluctuations have been documented in omnivorous voles and insectivorous shrews in Fennoscandia (Hansson & Henttonen 1988, Lindén 1988), Japan (Saitoh 1987), and the northeastern United States (Elias, Witham, & Hunter 2006). Strong cyclic fluctuations of

red-backed vole populations include suggest approximately a 4.4 year periodicity and cycles synchronous with population fluctuations of a sympatric generalist, white-footed mice (Elias, Witham, & Hunter 2006). Less support for shrew population cycles has been documented in the United States, where populations are hypothesized to be controlled by specialist predator pressure rather than intrinsic self-regulation (Korpimäki & Krebs 1996). Additionally, it is unclear how the treatment conditions influenced the invertebrate assemblage in BRF. While data on arthropod richness and density were collected, these data have not yet been published and therefore I can only speculate that they may have negatively impacted shrew abundance in Black Rock Forest following oak girdling.

Red-backed voles were most frequently encountered on control and 100% non-oak girdled plots. These treatments had significantly lower levels of coarse woody debris compared to 50% oak girdled and 100% oak girdled plots. In addition to altered forest floor conditions, red-backed voles are responsive to changes in forest canopy. Klenner & Sullivan (2009) identified red-backed voles as closed-canopy species, establishing a minimum threshold of 25% canopy cover to maintain pre-harvest abundance levels. Other variables including mesic microclimates (Powell & Brooks 1981) and percent ground cover (Yahner 1986) have been identified as key environmental characteristics which influence red-backed vole abundance. Moist conditions are necessary because red-backed voles demonstrate reduced drought-resistance compared to other forest dwelling mammals (Getz 1962; Getz 1968; McManus 1974). Increased ground vegetation may positively influence litter arthropods, a key component of red-backed vole diet (Ahlgren 1966; Vickery 1979). The canopy cover of the girdled treatment plots in BRF did not fall

below the species' minimum threshold established by Klenner & Sullivan (2009); however, it was lower compared to control plots. Reduced canopy cover coupled with other factors such as ground vegetation and soil moisture may have influenced red-backed vole abundance on 50% and 100% oak-girdled plots.

Northern short-tailed shrews, the third most commonly encountered species in this study, rely on soil moisture levels necessary to maintain 100% relative humidity inside their burrows (Whitaker & Hamilton 1998). For the majority of this study, shrews were closely associated with 50% oak girdled and 100% non-oak girdled plots. Association with these intermediately disturbed treatment plots was surprising because 100% non-oak plots had significantly lower soil moisture compared to 50% and 100% oak girdled plots. Shrew species are typically associated with reduced leaf fall and coarse woody debris (Fisher & Wilkinson 2005) and have been documented as the initial recolonizing species following conifer harvest (Parker 1989).

Although leaf fall did not significantly vary by treatment, coarse woody debris was significantly lower on 100% non-oak girdled plots, compared to 100% oak girdled plots. Changes to the litter layer of the forest floor greatly influence arthropod and plant diversity because litter acts as a buffer to changes in soil water content (Ginter, McLeod, & Sherrod 1979) and temperature (Ponge, Arpin & Vannier, 1993). In BRF following oak girdling, non-native earthworms invaded the study area and increased the rate of litter decomposition (W.S.F. Schuster, personal communications). The combination of altered forest floor conditions, changes in soil moisture and temperature, and decreases litter arthropod abundance may have influenced northern short-tailed shrew abundance on

intermediate disturbance plots and the overall decline in abundance over the course of the study.

Northern short-tailed shrews and the other unidentified Soricids displayed a delayed negative response to oak girdling; which differs from other studies, which have identified a positive response of shrews to clearcutting in multiple forest stand types, including conifer (Sekgoroane & Dilworth 1995; Steventon, MacKenzie, & Mahon 1998), hardwood (Kirkland 1977), and aspen (Probst & Rakstad 1987). The mode of disturbance in my study may have delayed the response of shrews. Unlike other forest disturbance studies that utilize prescribed fire and clear cutting, oaks in this study were girdled and left standing. Because the trees were not felled or immediately removed, changes to key habitat characteristics including leaf fall, coarse woody debris, and soil moisture may have been delayed as well. As the study continued, more trees fell and altered the microhabitat conditions, potentially, causing shrew abundance to decrease. This finding indicates that species such as shrews and voles may be the most appropriate species of interest for examining how small mammals respond to environmental disturbance such as tree mortality.

I hypothesized that small mammal species diversity would be influenced by key environmental variables, specifically leaf fall and coarse woody debris. Species diversity did not significantly differ by treatment and therefore was not influenced by increases in coarse woody debris due to girdling. An increase in species diversity, less than one year post girdling (2009), was temporary and may be the result of a 18 month time lag response of specialist species to forest disturbance, as seen in other small mammal studies

(Sullivan & Sullivan 2001; Klenner & Sullivan 2009). Significantly lower species diversity in 2011 and 2012 may be related to the high 2010 acorn mast. Although the 2011 white-footed mouse population estimate was not significantly higher than other years, the increased body mass indicates that mice may have been healthier and had an improved body condition in 2011.

Although species diversity did not vary by treatment, clear variation was observed in small mammal mass in response to the treatment conditions. This finding is supported by other studies that have observed similar decreases in body mass of related chipmunk species following habitat disturbance events (Tabeni & Ojeda, 2005; Meyer, Kelt, & North 2007). Reduced body mass in eastern chipmunks on 100% oak girdled plots may reflect an overall reduction in body condition of individuals on those treatment plots. Reduced body condition in eastern chipmunks may indicate that 100% oak girdled plots are a sink habitat for this species. Suboptimal habitat (ecological sinks) may support large numbers of individuals (Pulliam 1988), but these populations cannot be sustained without continued immigration from a source population (control plots). Due to the proximity of neighboring plots in this study, the eastern chipmunk populations on 100% oak girdled plots are not likely to go locally extinct because movement between plots was so common. Additionally, these sink habitats may serve as dispersal areas for juvenile or less dominant animals (Sullivan 1979) when population densities on optimal habitat become too high.

Environmental Change – The loss of oaks significantly altered the nitrogen cycling dynamics in BRF (Falxa-Raymond et al. 2012). From 2008 to 2010, foliar

nitrogen concentration increased by over 15% on 50% oak girdled treatments and over 30% on 100% oak girdled plots relative to the control. During this time, black birch growth rate increased by 641% on 100% oak girdled treatments (Falxa-Raymond et al. 2012). These findings suggest that an opportunistic tree species like black birch may have been able to quickly respond to the influx of nitrogen and light availability into the system to increase overall aboveground biomass within the ecosystem (Falxa-Raymond et al. 2012). The inconsistent changes observed in the measured environmental variables may have been the result of the rapid invasion of black birch on the oak girdled treatments in BRF. If black birch colonized the vacant niche space of the girdled oak trees, it may have influenced habitat characteristics that are important to small mammals including coarse woody debris, soil temperature, and soil moisture. Similar increases in black birch density has been seen across its geographic range in response to other disturbance events including forest thinning (Ward & Stephens 1996) and the decline in hemlock tree abundance (Kizlinski et al. 2002; Small, Small, & Dreyer 2005). When foundation tree species are replaced by early successional hardwoods such as black birch, alterations to important understory microclimatic conditions may occur. Orwig & Foster (1998) recorded rapidly decomposing deciduous leaf fall, increased coarse woody debris, and large canopy gaps following replacement of hemlocks with black birch. Although not statistically significant, leaf fall was lowest on 100% oak girdled plots in BRF, a finding that may be linked to black birch invasion. The microclimatic conditions of the forest floor are vital to small mammals, serving as refuge, foraging, and nesting habitat. Extensive changes to the forest floor, especially soil moisture and coarse woody debris,

coupled with the changes in soil chemistry noted above may negatively impact small mammal populations.

Soils play an integral role in the global carbon cycle, accounting for 60-70% of all CO_2 (carbon dioxide) released in forest ecosystems (Malhi, Baldocchi, & Jarvis 1999; Steinmann et al. 2004). Carbon dioxide released from soil, also known as soil respiration, is a common measure of decomposition and belowground biological activity (Parkin, Doran, & Franco-Vizcaíno 1996). Carbon dioxide flux rapidly declined following oak girdling at BRF (Levy-Varon, Schuster, & Griffin 2011).

Within two weeks of girdling on 100% oak treatments, soil CO_2 efflux decreased by 33%, before reaching the maximum decline (50%) after six weeks (Levy-Varon, Schuster, & Griffin 2011). This marked decline in soil respiration represents the loss of the autotrophic source of soil respiration – living plant roots and their mycorrhizal fungi (Levy-Varon, Schuster, & Griffin 2011). These roots and fungi are a prominent food source in the diet of many forest dwelling small mammals including mice, voles, squirrels, and chipmunks who consume large quantities of fungal spores (Merritt 2010).

Eastern chipmunk mass was significantly lower in 2010, possibly due to decreased availability of fungal food sources. The closely related long-eared chipmunk (*Neotamias quadrimaculatus*) has been found to rely heavily on fungi as a summer food source, especially in years of conifer cone crop failure (Tevis 1952, 1953, 1955). In my study, chipmunk body mass was significantly lower on 100% oak girdled plots, where decline in soil respiration was highest. Soil respiration in BRF recovered to pre-girdling measurements by 2011 (Schuster, unpublished data). This recovery is likely linked to the

641% increase in black birch growth rate discussed above. The increase in soil respiration may be linked to increased mycorrhizal fungi associated with colonizing black birch trees. Detecting fungi in the diet of small mammals in BRF is difficult, but if the small mammals relied on mycorrhizal fungi as a key component of their diets and soil respiration remained low for over two years, small mammal abundance may have been impacted on oak girdled treatment plots from 2008-2010.

Coarse woody debris provides refuge for small mammal nesting, foraging, and movement. Coarse woody debris was significantly higher on 100% and 50% oak girdled plots than non-oak and controls plots, because less basal area was removed on 100% non-oak girdled plots. I predicted increased generalist species abundance in response to increased volumes of coarse woody debris. The generalist species abundance responses in BRF are paradoxical to many forest disturbance studies which have found that white-footed mice and other chipmunk species preferentially choose areas with higher volumes of coarse woody debris (Greenberg 2002; Waldien, Hayes, & Huso 2006). Rather than responding positively to increased coarse woody debris in BRF, generalist species abundance showed no response to the treatment conditions. Although volume of coarse woody debris has been used as an effective predictor of species abundance of deer mice, red-backed voles, and multiple shrew species (Cary & Johnson 1995), in this study system, coarse woody debris was not a good predictor of small mammal species abundance. I hypothesize that coarse woody debris accumulation was delayed because trees were not felled when girdled. Additionally, because tree fall was not controlled, conditions on replicates of the same treatment may not have been equivalent.

Herbaceous vegetation cover is important to small mammals because it provides cover for movement, forage for mammals in the form of seeds and plant material, and serves as forage for small mammal invertebrate prey. Herbaceous vegetation cover was considerably higher on 100% oak girdled plots. Increased canopy openness, nitrogen (discussed above), and soil moisture on 100% oak girdled plots may have influenced the increased percentage of ground and mid-story plant growth on these plots. Higher coverage of herbaceous vegetation would suggest increased food availability (both plant material and invertebrates) to small mammals on 100% oak girdled plots. Increased small mammal abundance was not observed on 100% oak girdled plots, indicating that generalist small mammal species in BRF did not positively respond to increased vegetation cover. Like coarse woody debris, small mammal abundance may not have responded to changes in ground vegetation because changes in this variable relied on other changes to occur first. For example, ground vegetation cover could not increase until the trees fell, the canopy opened, and sunlight reached the forest floor. These preliminary changes may have delayed the effects of subsequent environmental changes.

Caveats – Ecosystem-level manipulative studies are rare in ecological research. Studies of this scale encounter many difficulties including appropriate spatial and temporal scales, experimental design issues such as randomization and replication of treatments, and identification of the most informative response variables to best capture ecological change (Smith 1999, Block et al. 2001). Shortcomings were prevalent in this study even though many of the complications listed above were addressed in the experimental design; it used a completely randomized block design consisting of equal

numbers of replicates, small mammals were monitored over five years, and it used annual abundance estimates, the appropriate demographic rate, as the response variable.

This study was part of a larger investigation; the overarching goal was to analyze all biotic responses to the experimental treatments. Because small mammals were not the focal organisms of the experimental design, experimental plot sizes and buffer strips were not large enough to prevent small mammal movement. Experimental treatment size in small mammal forest disturbance studies has been an area of contention in recent years (Smith 1999 in response to Von Trebra et al. 1998). Smith (1999) felt that Von Trebra et al. (1998)'s treatment size of 1.4 ha may have been too small to inform management decisions at a larger-scale. Even with an established buffer strip between each plot in this study, the most common species captured in this study have home ranges equal or larger in size to the experimental plots. Eastern chipmunks have a typical home range of 0.200 – 0.400 ha and white-footed mouse home range is 0.300 – 0.500 ha in New York (Saunders 1988). A significant proportion of eastern chipmunks (12%) and white-footed mice (32%) moved between treatment plots. With such a high percentage of captured individuals found on multiple plots and a lack of significant differences among treatments, the results may have been adversely affected by the proximity of neighboring treatment plots. Therefore, future studies should consider increasing plot size and having a larger buffer between plots. Additionally, pit-fall traps were not used in conjunction with Sherman live-trapping due to concerns about weather events impacting mortality of small mammals in pit-fall traps. Sherman traps are known to under sample shrews, voles, or other fossorial and litter-obligate species due to the small size of these species and

their lack of attraction to the bait (Churchfield 1990). Thus, the low number of shrews and voles captured in this study likely is an artifact of the sampling method, although they are usually rare even when sampled using alternative methods.

It is possible that the assumption of demographic closure may have been violated due to the movement of individuals between plots and possible births during the summer trapping season. However, many studies in the scientific literature support the selection of closed capture modeling, especially when the species of interest rarely survive longer than one season. White-footed mice and eastern chipmunks in New York breed in March and April of each year (Saunders 1988). While multiple breeding events may occur in other portions of these species' ranges, I did not observe an increase in juveniles at any point during the summer. Based on the lack of evidence for multiple breeding sessions and the literature support, I selected closed capture modeling.

Program MARK identified constant capture and time-variant recapture probabilities as the top closed capture likelihood model based on AIC_c for both white-footed mice and eastern chipmunks throughout the majority of the study. Extremely low inter-annual survival and low sample sizes prevented the use of Pollock's robust design model (Pollock 1990) to analyze survival, emigration, immigration, and capture rates. Low sample sizes and a lack of significant relationship between small mammal abundance and any environmental variables influenced my decision to analyze simplistic models focused only on treatment and time effects within each year. Even with the associated limitations, my results contribute to the understanding of small mammal species respond to extensive disturbance events and provide valuable information

regarding the demographic response of generalist small mammal species and species diversity to foundation tree mortality in eastern North American oak forests.

The environmental conditions of each plot were collected by multiple collaborators over the five years of this study. However, not all 10 variables were collected on the same time scale, leading to a reduction in sample size for some variables. For example, leaf fall data were collected at least once, but sometimes twice annually. Percentage of ground vegetation was only collected in 2010 and coarse woody debris data were only collected in 2010 and 2012. These discrepancies in data collection frequencies made it difficult to effectively quantify the environmental changes associated with each treatment.

Management Implications – The environmental conditions associated with the simulated pathogen attack in this study clearly demonstrate differences over time. Although small mammal abundance did not respond to the treatment conditions, other metrics such as body mass responded to the experimental treatments. Demographic modeling was not necessary due to the short lifespan of the species of interest and the multi-year design of this study. The dynamic nature of forest ecosystems can support species with varying behavioral plasticity; therefore these species may not indicate changes in environmental conditions. Specialist species such as red-backed voles and northern short-tailed shrews may be more appropriate indicators of environmental change based on their marked decline in abundance over the course of the study. Rather than intensively trapping for small mammals over a short period of time, managers may consider trapping in alternative years over a longer period of time to better understand the

response of small mammals to immediate disturbance events as well as the long-term response to changes associated with forest succession after a disturbance occurs. Additionally, trapping during alternative years may improve the ability to differentiate between cyclical population fluctuations and real responses to disturbances.

CONCLUSIONS

The objectives of this study were to investigate the demographic response of small mammals to extensive forest disturbance and to identify which habitat variables most influence these demographic parameters and overall species diversity. The results indicate that the small mammals of Black Rock Forest are generally resilient to stand-level mortality of foundation tree species. Abundances of both white-footed mouse and eastern chipmunks did not differ substantially among the experimental treatments of this study. Small mammal species diversity decreased over time, possibly due to cyclic population fluctuations of specialist species such as red-backed voles and northern short-tailed shrews. By increasing plot size and distance between plots and more extensively sampling the small mammal assemblage, I can improve the understanding of the impact of disturbance on these key ecological community members.

TABLES AND FIGURES

Table 1a: White-footed mouse abundance estimates based on full likelihood closed capture method of marking (*M*) and recapture (*C*) from 2008-2012 at Black Rock Forest, New York. The number of trapping months, or trapping occasions, the probability of being captured ($\hat{p}$) and recaptured ($\hat{c}$), and the estimated number of individuals ($\widehat{N}$ ± SE) are included for each treatment and year. Values of "N/A" indicate years when $\hat{p}$ and $\hat{c}$ were incalculable. Minimum number alive (MNA) abundance estimates were included in years when the top model did not include a treatment-variant abundance parameter.

Year	Treatment	Trapping Occasions	*M*	*C*	$\hat{p}$	$\hat{c}$	$\widehat{N}$	±SE
2008	Control	3	16	31	0.348	0.037	22	4.343
	100% Oaks	3	19	38	0.348	0.037	23	4.629
	50% Oaks	3	8	11	0.348	0.037	18	3.572
	100% Non-Oaks	3	29	58	0.348	0.037	26	5.579
2009	Control	5	8	11	N/A	N/A	8	N/A
	100% Oaks	5	14	24	N/A	N/A	14	N/A
	50% Oaks	5	12	25	N/A	N/A	12	N/A
	100% Non-Oaks	5	19	25	N/A	N/A	19	N/A
2010	Control	5	9	19	0.485	0.287	9	N/A
	100% Oaks	5	22	57	0.485	0.287	22	N/A
	50% Oaks	5	15	50	0.485	0.287	15	N/A
	100% Non-Oaks	5	20	80	0.485	0.287	20	N/A
2011	Control	4	46	101	0.354	0.516	46	N/A
	100% Oaks	4	58	141	0.354	0.516	58	N/A
	50% Oaks	4	58	153	0.354	0.516	58	N/A
	100% Non-Oaks	4	61	130	0.354	0.516	61	N/A
2012	Control	3	11	27	0.283	0.295	99	23.466
	100% Oaks	3	21	53	0.249	0.295	30	8.070
	50% Oaks	3	13	27	0.261	0.295	43	11.056
	100% Non-Oaks	3	18	40	0.251	0.295	33	8.673
Total							636	69.388

Table 1b: Eastern chipmunk abundance estimates based on full likelihood closed capture method of marking (*M*) and recapture (*C*) from 2008-2012 at Black Rock Forest, New York. The number of trapping months, or trapping occasions, the probability of being captured ($\hat{p}$) and recaptured ($\hat{c}$), and the estimated number of individuals ($\widehat{N}$ ± SE) are included for each treatment and year. Values of "N/A" indicate years when $\hat{p}$ and $\hat{c}$ were incalculable. Minimum number alive (MNA) abundance estimates were included in years when the top model did not include a treatment-variant abundance parameter.

Year	Treatment	Trapping Occasions	*M*	*C*	$\hat{p}$	$\hat{c}$	$\widehat{N}$	±SE
2008	Control	3	13	21	0.074	0.171	13	N/A
	100% Oaks	3	13	15	0.074	0.171	13	N/A
	50% Oaks	3	12	21	0.074	0.171	12	N/A
	100% Non-Oaks	3	12	13	0.074	0.171	12	N/A
2009	Control	5	47	89	0.393	0.206	150	2.327
	100% Oaks	5	26	72	0.393	0.206	132	1.752
	50% Oaks	5	33	60	0.393	0.206	128	1.607
	100% Non-Oaks	5	38	82	0.393	0.206	123	1.658
2010	Control	5	17	34	N/A	N/A	17	N/A
	100% Oaks	5	28	60	N/A	N/A	28	N/A
	50% Oaks	5	24	55	N/A	N/A	24	N/A
	100% Non-Oaks	5	20	46	N/A	N/A	20	N/A
2011	Control	4	8	12	N/A	N/A	8	N/A
	100% Oaks	4	2	2	N/A	N/A	2	N/A
	50% Oaks	4	11	11	N/A	N/A	11	N/A
	100% Non-Oaks	4	6	12	N/A	N/A	6	N/A
2012	Control	3	21	46	0.194	0.442	182	66.147
	100% Oaks	3	18	46	0.168	0.428	72	30.368
	50% Oaks	3	27	67	0.167	0.451	68	28.734
	100% Non-Oaks	3	21	44	0.172	0.454	82	33.630
Total							1103	166.223

Table 1c: Rare species abundance estimates based on minimum number alive (MNA) number of individuals from 2008-2012 at Black Rock Forest, New York. The number of trapping nights, or trapping occasions and the estimated number of individuals are included for each treatment and year.

Year	Treatment	Trapping Occasions	Northern Short-Tailed Shrew	Red-Backed Vole	Pine Vole	Meadow Vole	Unknown Soricid
2008	Control	3	4	8	0	0	0
	100% Oaks	3	7	0	0	0	0
	50% Oaks	3	8	0	2	0	0
	100% Non-Oaks	3	4	6	1	0	0
2009	Control	5	7	1	0	1	0
	100% Oaks	5	6	0	0	1	4
	50% Oaks	5	12	0	0	2	2
	100% Non-Oaks	5	12	0	0	1	0
2010	Control	5	3	1	0	0	0
	100% Oaks	5	0	0	1	0	0
	50% Oaks	5	0	0	0	0	0
	100% Non-Oaks	5	0	2	0	0	0
2011	Control	4	0	5	0	0	0
	100% Oaks	4	0	0	3	0	0
	50% Oaks	4	0	1	1	0	0
	100% Non-Oaks	4	1	4	4	0	0
2012	Control	3	0	0	0	0	0
	100% Oaks	3	2	0	0	0	0
	50% Oaks	3	0	0	0	0	0
	100% Non-Oaks	3	0	0	0	0	0
Total			66	28	12	5	6

Table 2: Significance levels of environmental variables from Wilcoxon rank sum test to examine variation based on treatment conditions and year in Black Rock Forest, New York, USA from 2008-2012. (*) denotes statistical significance.

Environmental Variable	**N**	***P*-value**	**Mean ± SD**
Variation by Treatment			
Air temperature (°C)	1333	0.829	20.96 ± 3.190
Soil temperature (°C)	1597	0.004*	17.66 ± 3.130
Soil moisture (θ)	1338	<0.001*	0.1798 ± 0.086
Leaf fall (g)	68	0.530	408.86 ± 228.720
Coarse woody debris (m^3)	24	<0.001*	18328.28 ± 26642.750
Canopy openness (%)	149	0.233	15.99 ± 5.990
Ground cover (%)	12	0.030*	12.75 ± 17.000
Variation over Time			
Air temperature (°C)	1333	<0.001*	20.96 ± 3.190
Soil temperature (°C)	1597	<0.001*	17.66 ± 3.130
Soil moisture (θ)	1338	<0.001*	0.1798 ± 0.086
Leaf fall (g)	68	<0.001*	408.86±228.720
Coarse woody debris (m^3)	24	0.001*	18328.28±26642.750
Canopy openness (%)	149	<0.001*	32.75±20.430
Winter prior precipitation (mm)	5	0.190	236.79 ± 205.780
Spring prior precipitation (mm)	4	0.670	279.95 ± 38.630
Acorn Mast	5	<0.001*	35200 ± 63183.610

Table 3: Pearson's correlation coefficients for relationships between full likelihood closed capture model estimated abundance and the measured environmental variables, years, and treatments in Black Rock Forest, NY from 2008-2012. (*) denotes significance at the 0.05 level (2-tailed), (**) denotes significance at the 0.01 level (2-tailed), and (c) refers to the lack of computation because at least one of the variables is constant.

Variable	Year	Treatment	White-footed Mouse	Eastern Chipmunk	Soil Temperature (°C)	Soil Moisture (θ)	Air Temperature (°C)	Coarse Woody Debris (m^3)	Canopy Openness (%)	Ground Vegetation (%)	Leaf fall (g)
Year	1	0	0.213	0.017	0.466*	-0.100	0.814**	0.461	0.264	.c	0.507*
Treatment	0	1	-0.390	-0.538*	0.015	0.129	-0.040	-0.060	0.041	0.074	-0.026
White-footed Mouse	0.213	-0.390	1	-0.115	0.419	-0.200	0.051	-0.477	-0.122	-0.661	0.137
Eastern Chipmunk	0.017	-0.538*	-0.115	1	-0.077	-0.073	-0.026	-0.430	-0.113	-0.574	-0.113
Soil Temperature (°C)	0.466*	0.015	0.419	-0.077	1	-0.554*	0.265	0.203	0.079	-0.307	0.268
Soil Moisture (θ)	-0.100	0.129	-0.200	-0.073	-0.554*	1	-0.255	0.582	-0.570	0.117	-0.592*
Air Temperature (°C)	0.814**	-0.040	0.051	-0.026	0.265	-0.255	1	0.746*	0.826**	0.268	.770**
Coarse Woody Debris (m^3)	0.461	-0.060	-0.477	-0.430	0.203	0.582	0.746*	1	-0.021	0.892	-0.945
Canopy Openness (%)	0.264	0.041	-0.122	-0.113	0.079	-0.57	0.826**	-0.021	1	0.421	0.677*
Ground Vegetation (%)	.c	0.074	-0.661	-0.574	-0.307	0.117	0.268	0.892	0.421	1	-0.991**
Leaf fall (g)	.507*	-0.026	0.137	-0.113	0.268	-0.592*	0.770**	-0.945	0.677*	-0.991**	1

Fig. 1: Map of the north slope experimental site in Black Rock Forest, Cornwall, NY, USA where small mammal trapping and habitat analysis was conducted from 2008-2012. Four treatments and three replicates of each were created on this 67,500 m^2. Study plots used in this experiment are inside the red box. Map source: Black Rock Forest Consortium.

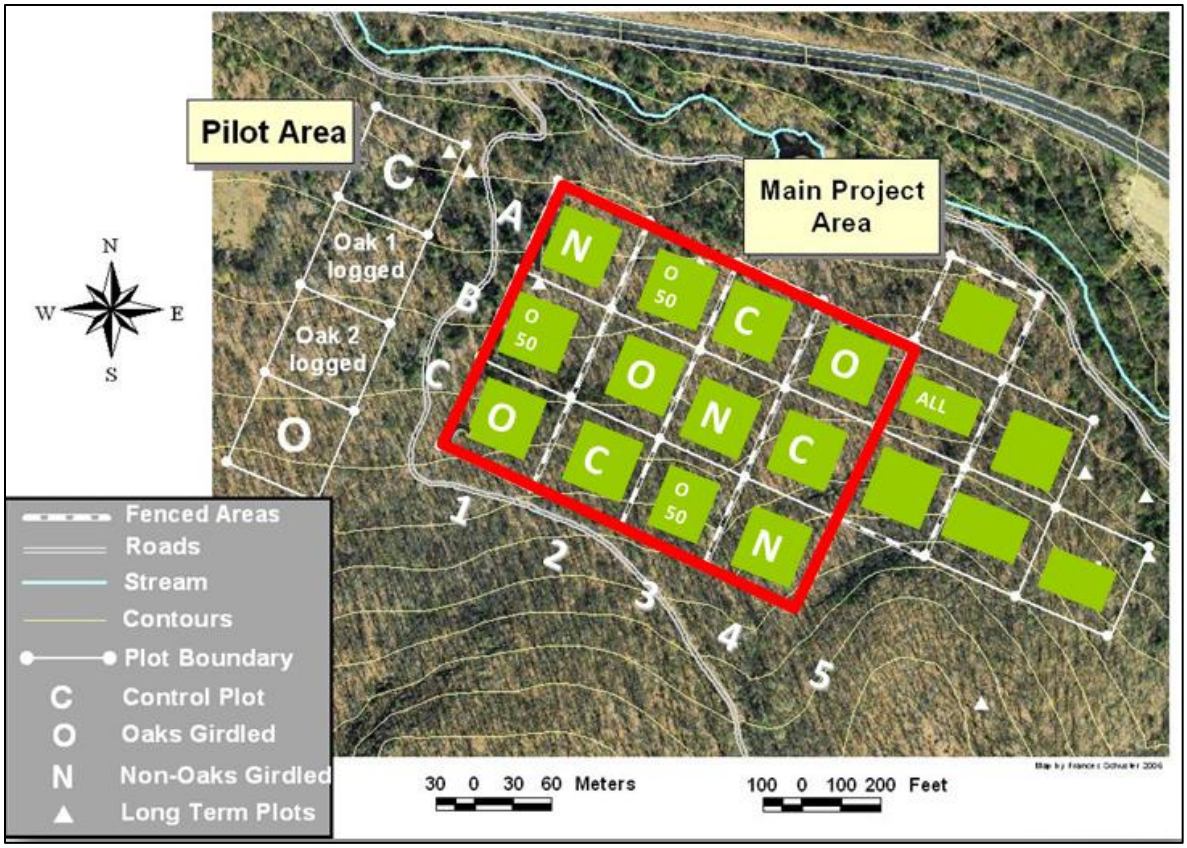


Fig. 2: Trapping web design and distance between adjacent trapping webs and plots for Sherman live trapping at Black Rock Forest, NY from 2008-2012.

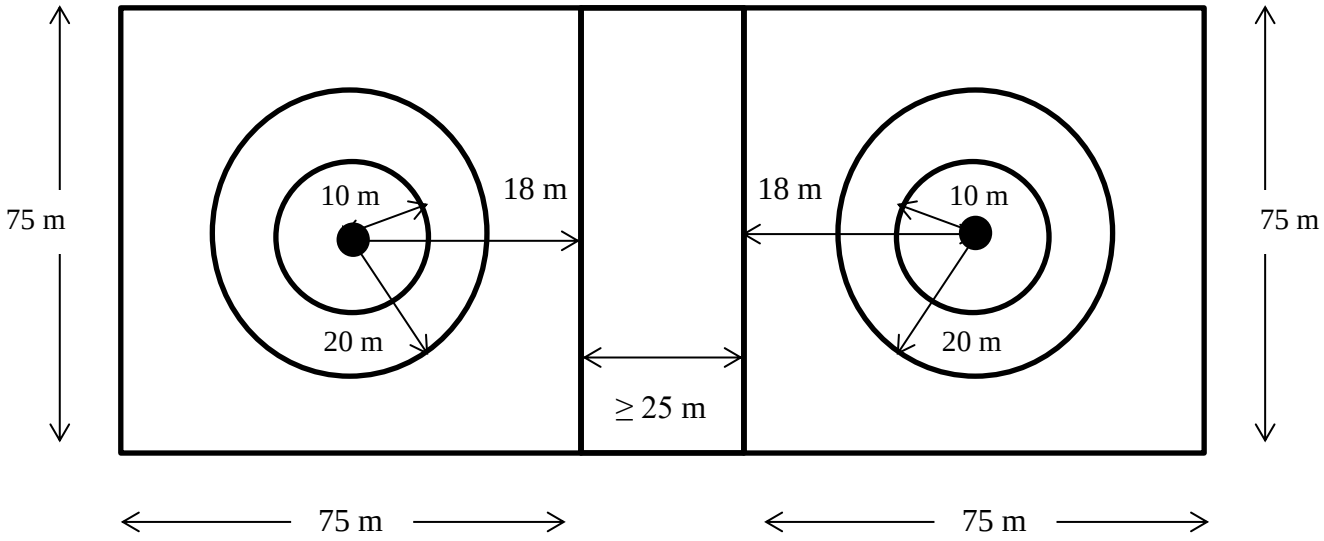


Fig. 3: Mean abundance estimates of eastern chipmunks and white-footed mice at Black Rock Forest, NY across all treatments from 2008-2012. Abundance estimates were real parameters included in full likelihood closed capture models in Program MARK.

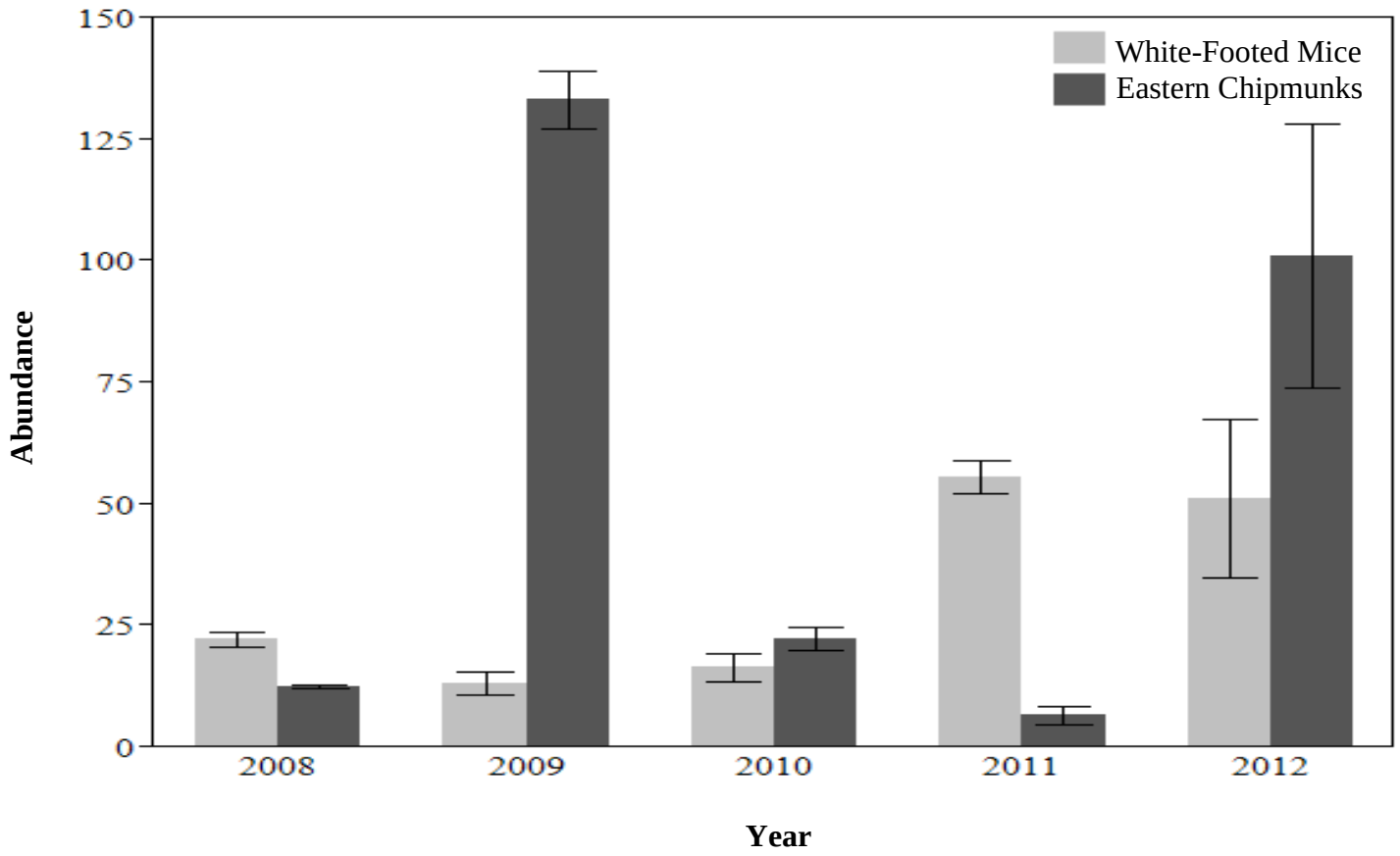


Fig. 4: Acorn mast at Black Rock Forest, NY from 2008-2012. Estimated acorn mast was 0 acorns per hectare in 2011 and 2012 at Black Rock Forest, NY.

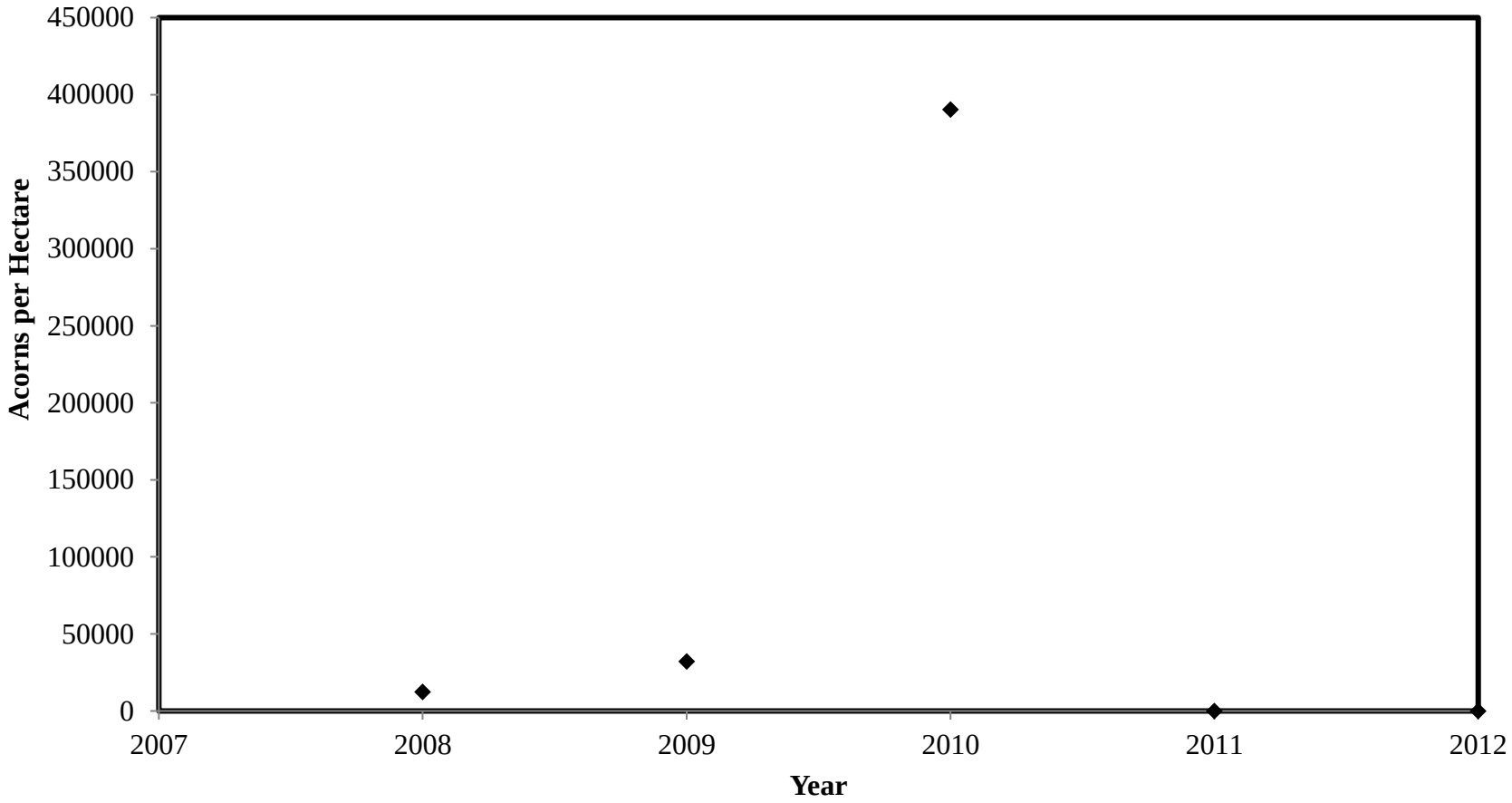


Fig. 5a: Canonical correspondence analysis (CCA) biplot demonstrating the relationships between the abundance of small mammal species and the environmental and treatment variables in the early years (2008-2009) of the study at Black Rock Forest, NY.

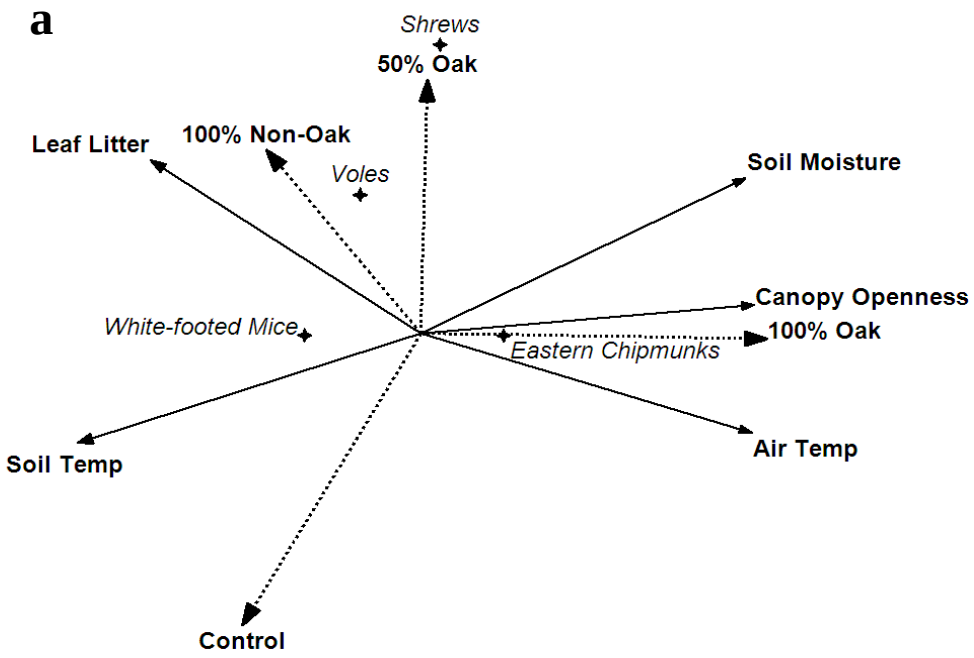


Fig. 5b: Canonical correspondence analysis (CCA) biplot demonstrating the relationships between the abundance of small mammal species and the environmental and treatment variables in the middle years (2010-2011) of the study at Black Rock Forest, NY.

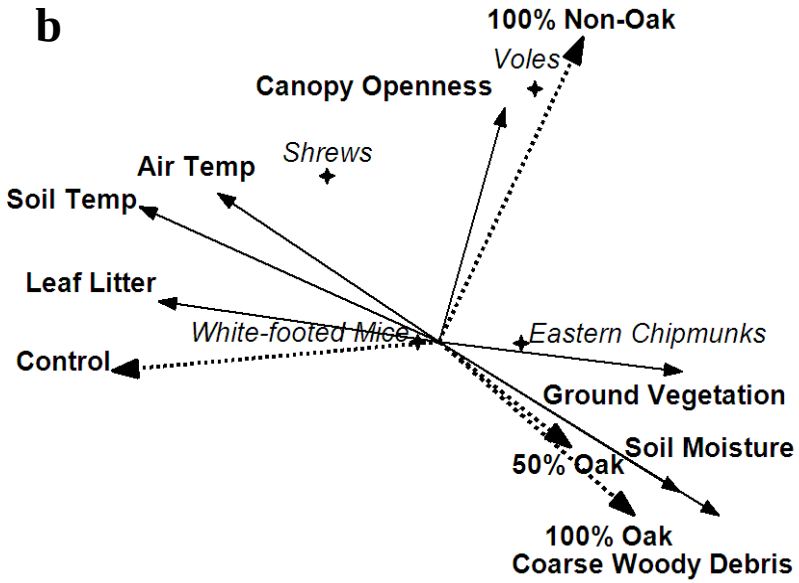
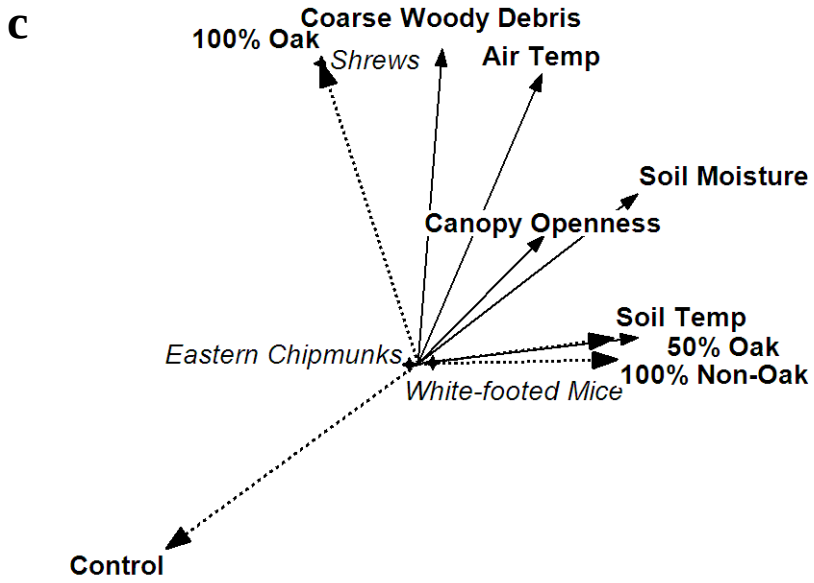


Fig. 5c: Canonical correspondence analysis (CCA) biplot demonstrating the relationships between the abundance of small mammal species and the environmental and treatment variables in the late stage (2012) of the study at Black Rock Forest, NY.



APPENDIX

Appendix 1a: Best fit initial capture (*p*) probability, recapture (*c*) probability, and population (*N*) models and model selection results for white-footed mice in Black Rock Forest, NY from 2008-2012. Model selection results include AIC_c, Δ AIC_c, AIC_c weight, model likelihood, and number of parameters (*K*). Bolded models indicate the top model based on AIC_c. "N/A" refers to years when low sample sizes prevented the estimation of all model parameters in all models of the candidate model set.

Year	Model	AIC*c*	Δ AIC*c*	AIC*c* Weight	Model Likelihood	*K*
2008	**{*p*(.)*c*(.)*N*(.)}**	**-96.542**	**0**	**0.758**	**1**	**3**
	{*p*(.)*c*(.)*N*(treatment)}	-94.256	2.286	0.242	0.319	6
2009	**N/A**	**N/A**	**N/A**	**N/A**	**N/A**	**N/A**
2010	**{*p*(.)*c*(time)*N*(.)}**	**30.041**	**0**	**0.890**	**1**	**6**
	{*p*(.)*c*(.)*N*(.)}	34.225	4.184	0.110	0.124	3
2011	**{*p*(.)*c*(time)*N*(.)}**	**-1002.578**	**0**	**1**	**1**	**5**
2012	**{*p*(.)*c*(.)*N*(treatment)}**	**-162.975**	**0**	**0.548**	**1**	**6**
	{*p*(.)*c*(time)*N*(treatment)}	-161.671	1.304	0.285	0.521	7
	{*p*(treatment)*c*(.)*N*(.)}	-160.602	2.372	0.167	0.305	6

Appendix 1b: Best fit initial capture (*p*) and recapture (*c*) probability models and model selection results for eastern chipmunks in Black Rock Forest, NY from 2008-2012. Model selection results include AIC_c, Δ AIC_c, AIC_c weight, model likelihood, and number of parameters (*K*). Bolded models indicate the top model based on AIC_c. "N/A" refers to years when low sample sizes prevented the estimation of all model parameters in all models of the candidate model set.

Year	Model	AIC*c*	Δ AIC*c*	AIC*c* Weight	Model Likelihood	*K*
2008	**{*p*(.)*c*(.)*N*(.)}**	**-146.237**	**0**	**1**	**1**	**3**
2009	**{*p*(.)*c*(time)*N*(.)}**	**-502.291**	**0**	**0.836**	**1**	**6**
	{*p*(.)*c*(.)*N*(treatment)}	-499.035	3.256	0.164	0.193	6
2010	**N/A**	**N/A**	**N/A**	**N/A**	**N/A**	**N/A**
2011	**N/A**	**N/A**	**N/A**	**N/A**	**N/A**	**N/A**
2012	**{*p*(.)*c*(.)*N*(treatment)}**	-305.231	**0**	**0.674**	**1**	**6**
	{*p*(treatment)*c*(.)*N*(.)}	-302.852	2.380	0.205	0.304	6
	{*p*(.)*c*(treatment)*N*(treatment)}	-301.801	3.431	0.121	0.180	9

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