Coupled effects of forest growth and climate change on small mammal abundance and body weight: results of a 39-year field study

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Abstract

1. In rapidly changing environments, the combined effects of climate change and forest stand changes—such as growth or regeneration—are altering the availability of resources, particularly in systems with pulsed resources like seed-masting. These environmental shifts can have cascading impacts on animal populations, ultimately reshaping ecosystem structure and function. However, relevant studies are rare as they require long-term monitoring of both seed supply and animal populations.
2. We investigated how temporal changes in resource availability (red oak acorns [*Quercus rubra*]) influence the demographics and physical traits of white-footed mice (*Peromyscus leucopus*) using a 39-year dataset from Maine, USA, which includes: mouse abundance and body weight, red oak tree size and acorn production, and seasonal temperatures.
3. Our analysis of 5,032 individual mice revealed a significant increase in both abundance (by 67%) and average body weight (by 15%) over four decades. We found that oaks produced more acorns as they grew, while warmer spring temperatures led to larger crops. This indicates that both forest growth and climate change have driven the increase in resource availability. The increase in acorn production was translated into higher mouse abundance and body weight. Notably, heavier mice also showed a higher probability of survival.
4. These results demonstrate that changes in food supply, driven by the combined effects of forest growth and climate change, have significant effects on animal population dynamics. Furthermore, given the important role of white-footed mice as seed

predators and dispersers, and disease vectors, these shifts have far-reaching implications for the ecosystem.

Keywords: Global change; Population dynamics; Red oak; Seed-masting; White-footed mouse

1 Introduction

Climate change is impacting animal populations through shifts in geographic range, abundance patterns (Dirzo et al. 2014), and phenotypic traits (Teplitsky et al. 2008; Merilä 2012). For example, altered rainfall in the Amazon is reshaping fish, bird, and mammal populations (Bodmer et al. 2017), while rising temperatures in subalpine habitats have led to an increase in mammal body weight (Ozgul et al. 2010). A key aspect of this impact is the change in the spatiotemporal patterns of resource availability, especially in systems with pulsed resources like mast-seeding, where tree seed production varies greatly from year to year (Yang et al. 2008; Hacket-Pain and Bogdziewicz 2021). Masting plays a crucial role in food webs and is strongly influenced by weather which makes it particularly vulnerable to climate change (Bogdziewicz et al. 2024). Shifts in seed supply driven by masting can significantly impact entire ecosystems (Touzot et al. 2023). The combined effects of climate change and resource shifts can cascade through ecosystems, potentially altering their structure and function (White 2008). Given these dynamics, research on how animal populations respond to climate change in environments with variable resources is increasingly important.

Variations in body weight as a response to climate change

Empirical evidence indicates that some populations are decreasing their average weight in response to warmer temperatures while others are increasing (review in Gardner et al.

2011). The documented mechanisms behind decreases include a reduction in growth rate (Ozgul et al. 2009), survival (Teplitsky et al. 2008), and lifespan (Hoy et al. 2017), all due to environmental stress associated with higher temperatures (Searing et al. 2023). Conversely, increases in weight are driven by increases in net primary productivity and food abundance due to warmer conditions leading to a longer foraging season and consequent increases in weight before the winter (Ozgul et al. 2010; Wereszczuk et al. 2021). Because body weight is a life-history trait with wide impacts on the demographic performance of populations (Visser 2008), understanding how body weight responds to changing environments is crucial for wildlife conservation.

Climate change effects on demographic rates

Assessing trends in abundance can help predict the “winners” and “losers” of global environmental change (Dornelas et al. 2019). The negative effects of climate change on species abundance, potentially leading to local extinctions, have been widely explored (e.g. Nally et al. 2009; Cahill et al. 2013; Dirzo et al. 2014). Conversely, some populations are increasing in abundance (Bowler et al. 2017), perhaps due to the direct effects of warmer temperatures on population growth (Deutsch et al. 2008) or indirect effects such as an increase in food availability (Touzot et al. 2020). Therefore, understanding temporal abundance patterns as a function of changes in temperature and food availability can provide important information for conservation.

Pulsed resources effects on animal populations

With or without climate change, food availability is often the dominant factor in pulsed ecosystems with periods of high availability followed by low periods (Yang et al. 2008). Pulsed resources are often responsible for enormous variations in animal population parameters including abundance (Elias et al. 2004), body weight (Nathoo et al. 2022), survival (Ruf et al. 2006), and reproduction (Boutin et al. 2006). One classic example of pulsed resources is mast seeding events – the pronounced interannual variability in seed production by perennial plants (Pearse et al. 2016). Mast-seeding events have major effects on many seed-consumer species, including small mammals (Ostfeld and Kessing 2000). Because of the close association between seeds and granivores, if masting patterns are disrupted, the consequences could range from constrained forest regeneration (Zwolak et al. 2022) to disease outbreaks (Schauber et al. 2005). As changes in masting patterns due to climate change are increasingly documented (Bogdziewicz et al. 2020a; Shibata et al. 2019; Foest et al. 2024), there is a pressing need to understand how altered masting patterns influence food webs (Touzot et al. 2023).

Forest growth and pulsed resources

Mast-seeding patterns depend both on forest age and weather (Pesendorfer et al. 2020, Szymkowiak et al. 2023). As young forest stands age, more trees enter the peak of their mast production, which ultimately slows down (Clark et al. 2021; Qiu et al. 2021). Mast-seeding patterns also depend on weather conditions (mainly temperature and precipitation) (Pesendorfer et al. 2020). Thus, both climate change and forest growth may modify the frequency and magnitude of mast-seeding events (Shibata et al. 2019; Bogdziewicz et al. 2020a). More frequent and/or more homogenous mast-seeding events could lead to an increase in animal density and improved body condition (Fig. 1) (Bogdziewicz et al. 2020a; Touzot et al. 2023).

Coupled effects of climate change and forest growth on small mammal populations

In many places both climate change and forest growth or regeneration are occurring simultaneously, making it challenging to parse these two effects on population parameters (Pesendorfer et al. 2020). However, to better predict how populations will respond to global change scenarios studies should consider both factors.

In this study, we report that a population of white-footed mice (*Peromyscus leucopus*) – an important seed predator and seed disperser in North American forests (Ostfeld et al. 1996) – is experiencing an increase in abundance and average body weight over four decades (1983 – 2021). This pattern is particularly interesting because the white-footed mouse population cycle is strongly affected by red oak (*Quercus rubra*) mast-seeding events (Elias et al. 2004), which in turn are affected by both climate change and forest stand age (Pesendorfer et al. 2020; Hacket-Pain & Bogdziewicz 2021). We tested whether changes in masting occurred during the four decades of monitoring, and whether these were responsible for changes in demographic parameters and phenotypic patterns of white-footed mouse population. Specifically, our objectives were to: 1) Investigate whether climate change and forest growth are driving changes in masting patterns and evaluate whether this affects the abundance and weight of white-footed mice, and 2) assess the consequences of abundance and weight increases for survival. We expect that the increase in temperature coupled with tree growth should increase the acorn supply, thus driving the observed increase in abundance and body weight (Fig. 1).

While we expect a positive influence of the increased body weight on individual's survival, the increase in population abundance should have a negative influence on survival.

To tackle these objectives, we used a 39-year-long monitoring of white-footed mouse abundance and weight, red oak acorn production, red oak tree diameter at breast height (DBH), and seasonal temperature. Our broad data collection allowed us to estimate the consequences of climate change and forest growth on resource availability and consumer population dynamics.

2 Material and Methods

2.1 Study area

From 1983 to 2021 we collected data on rodent abundance, seed production, and tree size in a 30-ha portion of the Holt Research Forest, Maine, USA (Fig. S1). This is a mature pine-oak forest (most trees are 90+ years old) where the dominant tree species are white pine (*Pinus strobus*), red oak (*Q. rubra*), and red maple (*Acer rubrum*). The dominant small mammal species include the white-footed mouse (*P. leucopus*), southern red-backed vole (*Myodes gapperi*), eastern chipmunk (*Tamias striatus*), and American red squirrel (*Tamiasciurus hudsonicus*). The target species for this study are white-footed mice and red oak. The Holt Research Forest is part of Maine's coastal climatic region and midcoast biophysical region. The average temperature in winter (January) is -12°C while in summertime the average temperature is 15°C (July). The annual mean precipitation is 1140 mm and the mean snowfall is 1880 mm.

2.2 Data collection and processing

2.2.1 White-footed mouse

To capture mice, we established six parallel trap transects 100 m apart (Witham et al. 1993). Each transect measured 400 m in length and had 24 trap stations, totaling 144 trap stations (Fig. S1). Trap stations were 16 m apart within each transect and contained two Sherman traps, totaling 288 traps. Trapping was conducted once a year in August. Traps were active for five consecutive nights and were checked daily between 6:00 and 10:00 h. We baited traps with a mixture of rolled oats and peanut butter. We also included a 5.1 x 5.1 cm pad of pressed cotton for bedding and insulation. We marked all captured mice with unique metal ear tags and recorded their age, sex, and weight following standard methods (Kays and Wilson 2009). Animal handling procedures were approved by the University of Maine Institutional Animal Care and Use Committee (IACUC protocol A2020-05-05) and Maine Department of Inland Fisheries and Wildlife (permit no. 2020-562).

We calculated annual white-footed mouse abundance by summing the number of unique individuals captured per year, and we calculated annual body weight by averaging the weight of all individuals per year. Importantly, we compared average weight between age categories (juveniles vs adults), sex (males vs females), and recaptured individuals between years to ensure our estimates were not affected by sampling artifacts (Fig. S2). We did not measure the body weight of 183 individuals, so we assigned them the average weight to keep them in the abundance and survival models (see below); they only represented 3.6% of the data.

2.2.2 Red oak acorns

To measure annual acorn production, we deployed seed traps with two sampling methods over the years (Fig. S1). From 1983 to 1990 we evenly distributed large traps (sample area = 0.5 m^2) in the 30-ha area (n = 29), and acorns were collected monthly (Witham et al. 1993). From 1988 to 2021 we deployed a higher number (n = 264) of smaller traps (sample area = 0.042 m^2) along the Sherman trap transects and at 10-m intervals along two east-west 600 m transects, and acorns were collected once a year in May (Witham et al. 1993). The annual records of seed production obtained via these two methods were highly correlated (cor = 0.92; $p < 0.01$) and therefore they are comparable. We estimated annual red oak acorn production (density of seed production: number of seeds/m^2) by summing the number of acorns captured in all traps per year and dividing by seed trap area to account for different sample efforts throughout the project. We also estimated acorn interannual variation by calculating the coefficient of variance (CV) of seed production for each moving 4-year window (see Data Analysis for further details).

2.2.3 Red oak trees

To measure tree growth, we conducted timber inventory in five years (1984, 1988, 1996, 2007, and 2020) in which all red oak trees with a DBH > 9.5 cm were measured in 1 ha blocks (Fig. S1). The number of surveyed blocks varied from 17 to 30 over the years, but our sample size was always large, with at least 2,000 trees per year (Fig. S3). We marked all measured trees with a unique tag starting in 1988 but we only included trees that were alive in the analysis (n = 5,112 trees). Most live trees (86%) were re-measured in following inventories. In 1984, we measured 4,532 trees but they were not tagged.

We estimated tree growth using a 2-step process. First, we averaged the DBH values of all measured live trees per inventory year. Then, we calculated the difference in the average DBH between years when timber inventory was conducted and divided it by the number of years between inventories. This yielded the average annual DBH increment of red oak trees.

2.2.4 Temperature

We obtained maximum and minimum temperature for each day of the year throughout our study period (1983 - 2021) from a weather station in Newcastle, Maine, located 28 km from the Holt Research Forest. With these daily measurements, we calculated the average, minimum, and maximum temperature per year, which were correlated, so we elected to use the minimum temperature in our analysis as warming winters and springs can significantly affect seed masting (Koenig et al. 2015) and animal species (Rowe et al. 2015). We calculated the annual average minimum temperature by averaging daily minimum measurements throughout each year. Because seasonal patterns may play an important role in pulsed resource ecosystems (Koenig et al. 2015), we also calculated seasonal average minimum temperatures by averaging monthly measurements for each season (winter = December – February, spring =March–May, summer = June – August, autumn = September – November).

2.3 Data analysis

2.3.1 Regression models

To investigate temporal associations between white-footed mouse population parameters (abundance and weight) and biotic (acorn production) and abiotic (temperature) factors we performed regression models. We constructed sets of models for each response variable: 1) mice abundance and 2) mice weight. For abundance, we performed generalized regression models with Poisson distribution, and for the body weight, we performed linear regression models with Gaussian distribution, and weight values were log-transformed to meet normality assumptions. The predictor variables for both sets were red oak acorn production, acorn interannual variation, minimum temperature (annual and seasonal), and time (year). All variables were the averages on a moving 4-year window with 1-step overlap (Bogdziewicz et al. 2023). For example, for time window 1 we averaged the values for years 1983 to 1986, for time window 2 we averaged the values for years 1984 to 1987, and so on. For estimating interannual variation in acorn production for the moving windows, we also calculated the standard deviation (sd) of each window to apply the formula of the coefficient of variation CV = sd/mean. The moving window average was done to better capture temporal trends in the data and smooth over the large interannual variation that is associated with masting and, consequently, mice population dynamics (Bogdziewicz et al. 2023). We understand that the step length for the window selection is arbitrary, and thus we checked for potential differences by using other time windows and they provided results consistent with our chosen 4-year windows. In our models, time represents the windows and it was a continuous variable ranging from 1 to 34. All predictor variables (acorn production, acorn interannual variation, annual and seasonal minimum temperature) except time were z-standardized prior to the analysis. All variables in our models are continuous, including acorn production, because few plant species have binomial seed production and thus treating it as a numerical factor is more appropriate (Kelly 1994).

To evaluate temporal changes in acorn production and acorn interannual variation as a function of changes in tree size and temperature we performed a set of linear regression models with a Gaussian distribution, and again log-transformed the variables to meet normality assumptions. We constructed sets of models for each response variable: 1) acorn production and 2) acorn interannual variation. Predictor variables were red oak DBH, minimum temperature (annual and seasonal), and time. All variables were the averages on a 4-year window. We also estimated the effect of tree size and temperature on acorn production and interannual variation using a 10-year window, which produced qualitative similar trends (Table S1).

We followed the information-theoretic approach to model selection using the Akaike information criteria (AIC) to rank competing models. The inference was made using models within 5ΔAIC from the top model. We first tested single variable models (i.e. with one predictor), then tested additive models if more than one model ranked 5ΔAIC above the null model and if predictors were not correlated (i.e. cor > 0.5). Predictors were not correlated except for time and temperature (annual and seasonal) and time and red oak DBH and thus we did not include these variables in the same model.

To perform these analyses, we used program R version 4.2.3 (R Core Team 2023) with the packages RcppRoll (Ushey 2018) and AICcmodavg (Mazerolle 2023).

2.3.2 Survival models

To assess the consequences of body weight on mouse survival probability, we estimated monthly apparent survival using robust design models with the Huggin's estimator using the capture-recapture data. Robust design models allow us to account for capture, recapture, and immigration probabilities. We used the step-down approach to determine the top model for each parameter (capture, recapture, emigration, and survival) sequentially (Lebreton et al. 1992). Following Dri et al. (2022), we modeled capture and recapture probabilities as equal (p =c) and varying as a function of body weight, and emigration probabilities as equal (random temporary emigration γ′ = γ″) and they were held constant. We estimated survival probability as a function of abundance, body weight, and time (with no window). We also tested an interaction between body weight and time and abundance and time to assess whether these associations were density-dependent.

We only included live individuals that could potentially be recaptured, totaling 4,935 analyzed mice. For individuals with more than one weight measurement, we used the individual's average weight. We conducted this analysis with the program Mark (White and Burnham 1999) using R-Mark interface (Laake 2013).

3 Results

Throughout the 39 years of the project, we captured 5,032 individual white-footed mice. Annual abundance varied from one to 435 individuals and their annual average body weight ranged from 17.7 to 23.2 g (mean = 20.5 ± 1.3) (Fig. 2). Annual red oak acorn production (summed over all traps) varied from zero to 20 acorns/m^2 per year (Fig. 2). The annual average minimum temperature increased from 3.3°C in 1983 to 4.6°C in 2021 representing a 1.2°C increase in 39 years (Fig. 2).

Through our regression models, we found that the white-footed mouse 4-year average abundance differed 2.4-fold between years with low acorn production (non-mast years) and years with high acorn production (mast-years) ($\beta = 0.21$, se = 0.01, $p < 0.01$; Table 1). There was also a positive trend in mice abundance, which increased by 1.6-fold from 1983 to 2021 ($\beta = 0.01$, se = 0.006, $p = 0.01$). However, when acorn production and time were combined in an additive model, the time effect in the model was no longer significant ($\beta = 0.001$, se = 0.006, $p = 0.80$) (Fig. 3A & B; Table 1), suggesting that the increase in rodent abundance is mostly explained by the increase in acorn production over time rather than by other time-varying environmental variables.

The top-ranked regression model for white-footed mouse body weight (4-year average) included a positive relationship with red oak acorn production. The average body weight of mice increased 1.2-fold as a function of acorn production, from 20.2 g in non-mast years to 21.8 g in years with high production ($\beta = 0.02$, se = 0.004, $p < 0.01$). The model also included a positive effect of time as individuals increased their average weight by 15% over the four decades of the study ($\beta = 0.003$, se = 0.0004, $p < 0.01$) (Fig. 3C & D; Table 1). Models including temperature (annual and seasonal), and the additive effect of temperature and acorn production scored above the null model but were not included in the final model set (i.e. $\Delta AIC > 5$) (Table S2).

The top-ranked model for the monthly survival probability of white-footed mice included a negative interaction between body weight and time, indicating that the positive effect of body weight on survival was weakening over time ($\beta = -0.006$, se = 0.003). The model containing only body weight was within $5\Delta AICc$ suggesting that body weight is the main predictor of survival (AICc weight = 0.22; Table 1). Mice monthly survival was 53% for individuals with low body weight (14.5 g) and 86% for individuals with high body weight (26.2 g; $\beta = 0.40$, se = 0.08). We did not find a temporal trend in the survival probability ($\beta = -0.0008$, se = 0.002) (Fig. 4; Table 1). The interaction between abundance and time had a negative effect on survival ($\beta = -0.01$, se = 0.003) but this model ranked below 5ΔAIC (Table S2).

The regression models for acorns showed that red oak acorn production almost tripled (2.9-fold increase) with increasing red oak DBH ($\beta = 0.29$, se = 0.06, $p < 0.01$) (Fig. 5; Table 1). The model including climatic effects (i.e. minimum temperature) on acorn production ranked lower than the null model. The acorn interannual variation was positively related to the increase of minimum temperatures in the spring ($\beta = 0.26$, se = 0.07, $p < 0.01$). The model including a temporal effect did not rank within 5ΔAIC, and thus the spring temperatures explain the acorn interannual variation without a time trend.

4 Discussion

Understanding how global change influences demographic and phenotypic parameters is key to developing effective conservation actions. Here, we compared the relative effects of climate and forest growth on observed increases in abundance and weight of a white-footed mouse population, an important seed predator and disperser in North America (Ostfeld et al. 1996). We found evidence for two, non-mutually exclusive mechanisms affecting trends in mice populations: increased tree size and increasing spring temperature, both of which were positively associated with acorn supply. Tree DBH was a strong predictor of acorn production (Fig. 5A), and acorn production was a strong predictor of mice abundance (Fig. 3A) and weight

(Fig. 3C). Moreover, the minimum spring temperature increased the interannual variation in acorn production through increasing the size of mast peaks. Time had a strong effect on body weight as its effect was still significant after accounting for other drivers. This suggests that other mechanisms, such as forest maturity, contributed to the increase in body weight. However, this was not true for abundance – the effect of time was significant only when it was the only variable included in the model indicating that increasing acorn production fully explains the abundance patterns. Together, our study offers rare documentation of how long-term changes in seed production patterns affect vertebrate seed consumers.

Forest growth effects on abundance and body weight

Acorn production was positively associated with both abundance and body weight trends in white-footed mice. This might indicate that a major mechanism driving the increase in abundance and body weight of mice is forest growth and an associated increase in seed supply. As forest stands mature, larger trees produce more seeds (Clark et al. 2021; Qiu et al. 2021; Szymkowiak et al. 2023). Seed-masting events are recognized as one of the most important factors driving population fluctuations in small mammals (Krebs et al. 1996), so it is not surprising that increasing seed supply is a strong predictor of their long-term population dynamics. Importantly, however, masting is also influenced by weather conditions, and thus temperature also plays a relevant role in changes in the masting process (Shibata et al. 2019; Hacket-Pain and Bogdziewicz 2021), ultimately modifying animal populations.

Climate change effects on abundance and body weight

We found that the mean temporal increase in the acorn interannual variation is driven by the increase in spring temperatures. This is a superficially surprising result because phenology synchrony predicts that under higher spring temperatures, the interannual variation in acorn production should decline (Koenig et al. 2015). Specifically, years with high spring temperatures are associated with higher flowering overlap among trees, higher pollen transfer, and increased acorn set (Koenig et al. 2015, Bogdziewicz et al. 2020b). In contrast, cold springs are associated with asynchronous flowering and pollination failure. Thus, spring warming should lead to more frequent and stable acorn production, lowering the interannual variation (Koenig et al. 2015). In our study system, the increase in acorn interannual variation is associated with masting events getting larger (i.e. more seeds are being produced in mast years) while the non-mast years still produce similar quantities of acorns (Fig. S4). We speculate that improved conditions for pollination combined with relaxed resource limitation driven by warmer climate result in larger crops (Bogdziewicz 2022). This implies that climate change has an indirect effect on the masting-rodent dynamic by modifying red oak acorn masting with cascading consequences for animal population dynamics.

Consequences of abundance and body weight on survival

The consequence of higher body weight is an increase in individual survival (Fig. 4A), which in turn can potentially increase population abundance. Body weight is a well-known predictor for survival (Rödel et al. 2004; Cox and Cresswell 2014; Brehm et al. 2024), particularly in the climate change context in which heavier individuals better cope with changes in the environment (Barbraud and Weimerskirch 2001; Ozgul et al. 2010). Here we go a step further by providing empirical evidence that in a pulsed resource system, resource availability has increased over time, leading to higher numbers of heavier mice. Potential consequences of this phenomenon may include a higher dispersal rate of larger seeds since heavier individuals can carry larger seeds and to a farther distance (Muñoz and Bonal 2008; Celebias et al. 2024) and a higher incidence of diseases since heavier mice are more susceptible to be infected by *Borrelia burgdorferi* – the pathogen of Lyme disease (Yen et al. 2024).

Surprisingly, however, our models indicate that survival probability is constant over time, despite the strong link between weight and survival, and weight and time. This discrepancy could be related to predation pressure that may increase mortality when mice density is higher (Krebs et al. 1996). Higher mortality in peak density years is corroborated by our models, as the interaction term between abundance and time showed a negative trend, though this model ranked below 5ΔAIC (Table S2). This result suggests that both external factors (e.g. predation and disease) and intrinsic factors (e.g. density-dependent effects due to population cycle) may be limiting survival (Krebs et al. 1996; Andreassen et al. 2013). As a consequence, currently heavier mice share a similar survival probability as lean mice in the past.

Limitations of our study and future directions

Our unique long-term empirical data allowed us to test the effects of forest growth and climate change on food availability and the cascading effects on animals. We were able to study 10 full population cycles of white-footed mice, represented by a sample size of over 5,000 individuals. We also had robust data on food resources from 293 seed traps, and forest growth from over 5,000 red oak trees in a 30-ha area in four decades.

Although we only recorded female pregnancy status starting in 2016, our raw data indicates that the number of captured pregnant females was stable between 2016 and 2021 (Table S3) and thus it is unlikely that our observed temporal trend in body weight is caused by higher capture rates of pregnant females in later sessions. This is further corroborated by the fact that both males and females in our study area are increasing in body weight (Fig. S2). We also acknowledge that we did not have data on body length to calculate body condition – a more informative determinant of fitness (Peig and Green 2009) – and hence we cannot properly untangle whether individuals are heavier or just older. Interestingly, only adult individuals show an increase in weight over time whereas juveniles show no temporal trend (Fig. S2). This could be because the juvenile stage is relatively short for white-footed mice (about 44 days) and most juveniles are already adults by the end of summer/beginning of fall (Lackey et al. 1985). Future studies should include the body condition variable and also look deeper into the reproductive status of individuals.

Implications and conclusions

The observed positive trends in abundance and weight of white-footed mice, driven by indirect effects of mature forests and warmer temperatures have important implications for the ecosystem, from forest composition to disease outbreaks. For example, larger and more abundant mice may consume a higher proportion of acorns, modifying forest composition and structure (Zwolak et al. 2022). Indeed, rodents are important seed dispersers contributing to forest regeneration (Jensen and Nielsen 1986; Vander Wall 2010), while a higher abundance of rodents could mean that more seeds are predated than dispersed displaying an antagonist interaction between rodents and seeds (Zwolak et al. 2024). Furthermore, rodents are natural reservoirs for many diseases including Lyme disease (Schauber et al. 2005). Changes in masting patterns could allow a more stable host base for ticks during white-footed mouse population cycles, creating a higher occurrence of diseases overall and accentuating concerns for human health.

Here we show evidence for two non-mutualistic mechanisms behind population dynamic patterns in a pulsed resource forest. We found a slightly stronger effect of forest growth than climate change on a white-footed mouse population, whereby the increase in tree size increases acorn production, creating a cascading effect on seed-consumer animals via the increase in abundance and body weight, ultimately increasing individual’s survival probability. This chain is happening during climate change, so the increase in temperature over time plays a secondary role. Nonetheless, maturing forests may be overriding the effects of climate change in our study system. Altogether, our results suggest that changes in food supply driven by forest growth and climate change have major effects on animal demographic patterns. Studies on the ecological consequences of climate change should carefully consider the role of co-occurring natural processes.

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Table 1: Top-ranking regression models for white-footed mouse abundance and body weight, acorn production and interannual variation, and top-ranking survival model for white-footed mouse using robust design with Huggin's estimator. Only models within 5ΔAIC from the top model are shown. The candidate models for abundance and weight included the following predictors: red oak acorn production and interannual variation of production (CV; coefficient of variation), minimum temperature (annual and seasonal), and time, while for survival it included abundance, body weight, and time. The candidate models for acorn production and interannual variation of production included red oak DBH, minimum temperature (annual and seasonal), and time as predictors. Acorn = red oak acorn production, time = number of time windows, DBH = red oak tree DBH, spring temp = spring minimum temperatures; k = number of parameters, ΔAICc = Delta Akaike Information Criterion; AICcWt = Akaike weight. Data were collected at the Holt Research Forest from 1983 to 2021.

Response	**Predictors**	**K**	**ΔAICc**	**AICcWt**	**p**	**R^2**
Abundance	acorn	3	0.00	0.76	< 0.01	0.41
	acorn + time	4	2.35	0.24	< 0.01	0.40
Body weight	acorn + time	4	0.00	1	< 0.01	0.85
Survival	body weight * time	7	0.00	0.77		
	body weight	5	2.41	0.22		
Acorn production	DBH	3	0.00	0.60	< 0.01	0.33
	time	3	0.87	0.39	< 0.01	0.32
Acorn interannual variation (CV)	spring temp	3	0.00	0.94	< 0.01	0.24

Figures

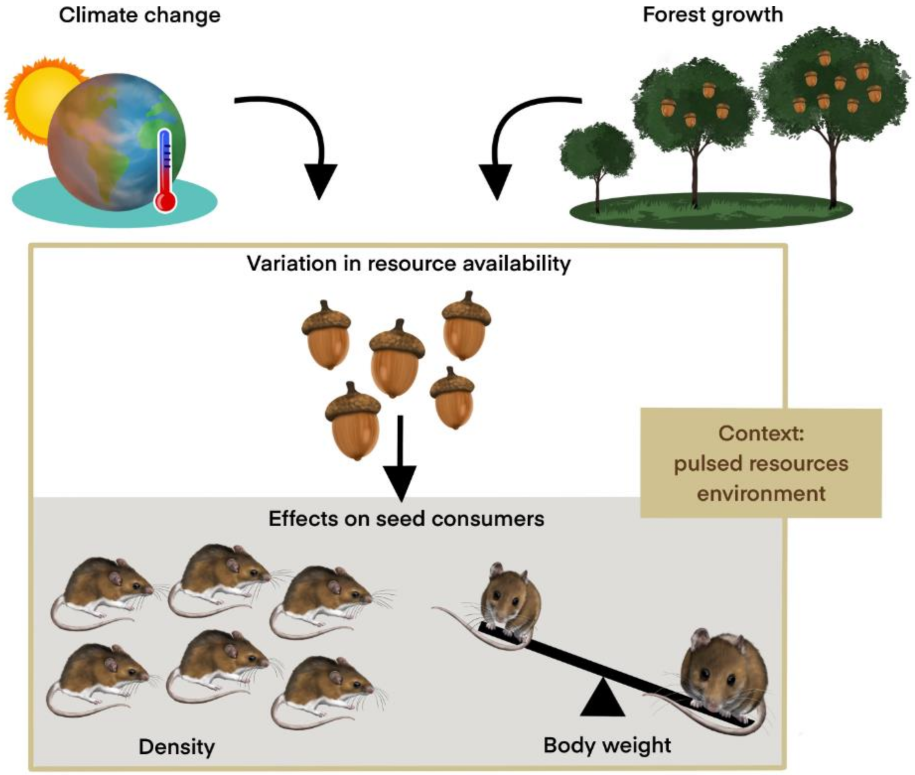

Fig. 1: Conceptual framework of the study. Both climate change, represented by the increase in temperature, and forest growth, represented by the increase in tree size, can affect seed consumer's abundance and body weight via the increase in resource availability, represented by acorn production.

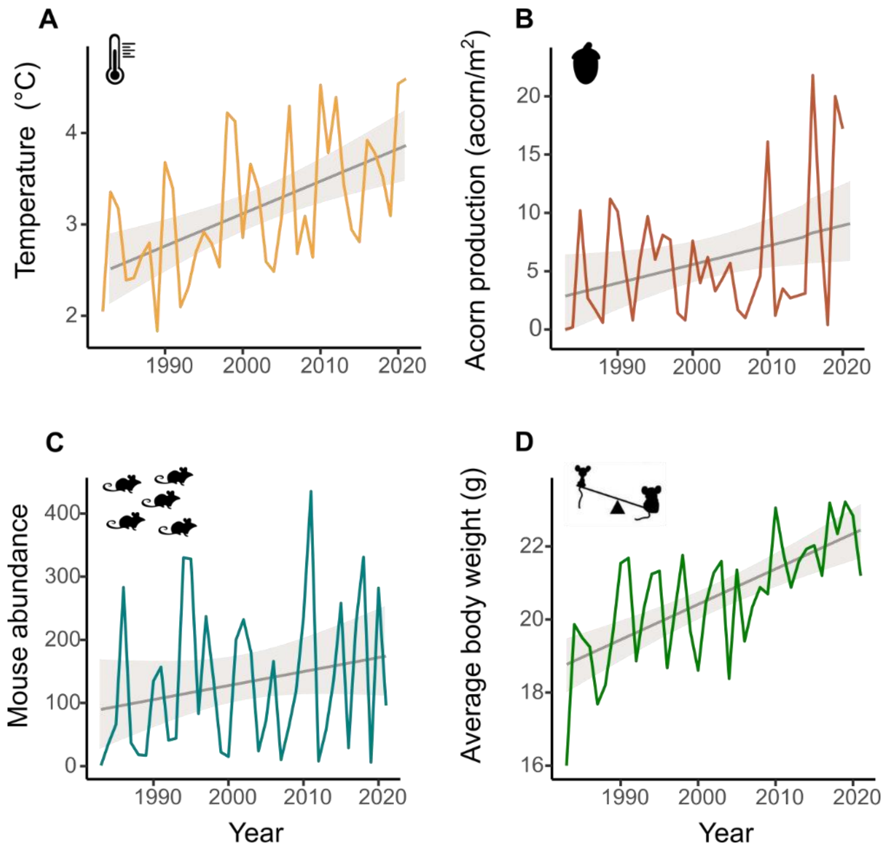

Fig. 2: Observed patterns of increase in **(A)** annual minimum temperature, **(B)** acorn production, **(C)** white-footed mouse abundance, and **(D)** body weight in the Holt Research Forest, Maine, US. Data were collected between 1983 and 2021 where 5,032 individual white-footed mice and 2,190 acorns were sampled over a 30-ha forest area. Gray lines indicate the prediction from linear regression models and shaded areas are the 95% confidence intervals. Colored lines are an interpolation of annual observations: temperature and body weight are annual averages, abundance is the sum of all mice caught per year, and acorn production is the total acorn density per year.

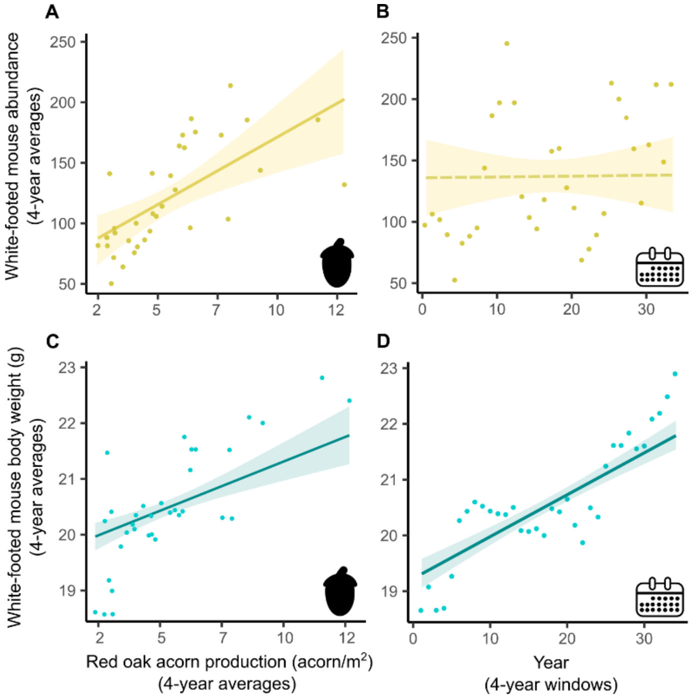

Fig. 3: Estimated white-footed mouse abundance and body weight patterns from the top-ranked regression models. **(A)** White-footed mouse abundance increased with red oak acorn production, **(B)** but the temporal trend disappeared once the trend in acorns was accounted for. **(C)** Body weight increased with red oak acorn production, **(D)** and with time (4-year windows) – even after accounting for the effects of increased acorn supply. Time was set constant at its mean value for the acorn prediction plots, while acorn production was set constant at its mean value for the time prediction plots. Variables were measured annually but were included in the models as averages on a moving 4-year time window (plotted as points). Body weight values were log-transformed in the models and back-transformed for visualization. Ribbons in the figure indicate 95% confidence intervals. The dashed line represents a non-significative association. Data were collected in the Holt Research Forest, Maine, USA, between 1983 and 2021, where 5,032 individual white-footed mice and 2,190 acorns were sampled.

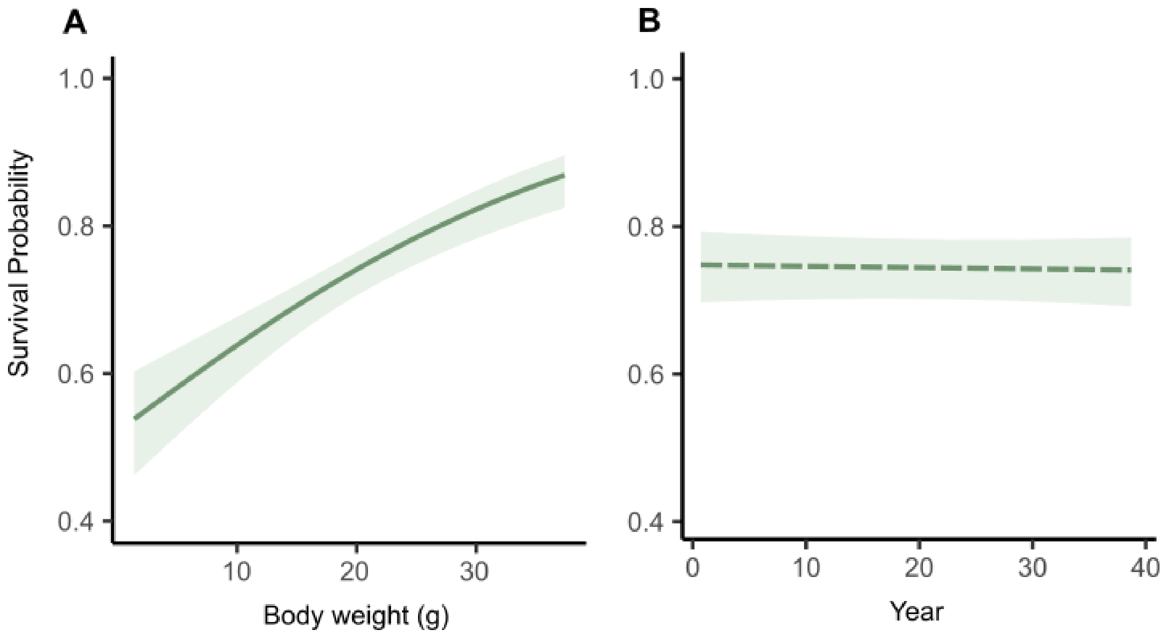

Fig. 4: Probability of monthly survival of white-footed mouse estimated using robust design models with the Huggin's estimator. Mice survival **(A)** increased with body weight but **(B)** there was no temporal trend. Body weight and time were modeled separately. Ribbons indicate 95% confidence intervals. The dashed line represents a non-significative association. Data were collected in the Holt Research Forest, Maine, USA, between 1983 and 2021, where 4,935 live individual white-footed mice were sampled.

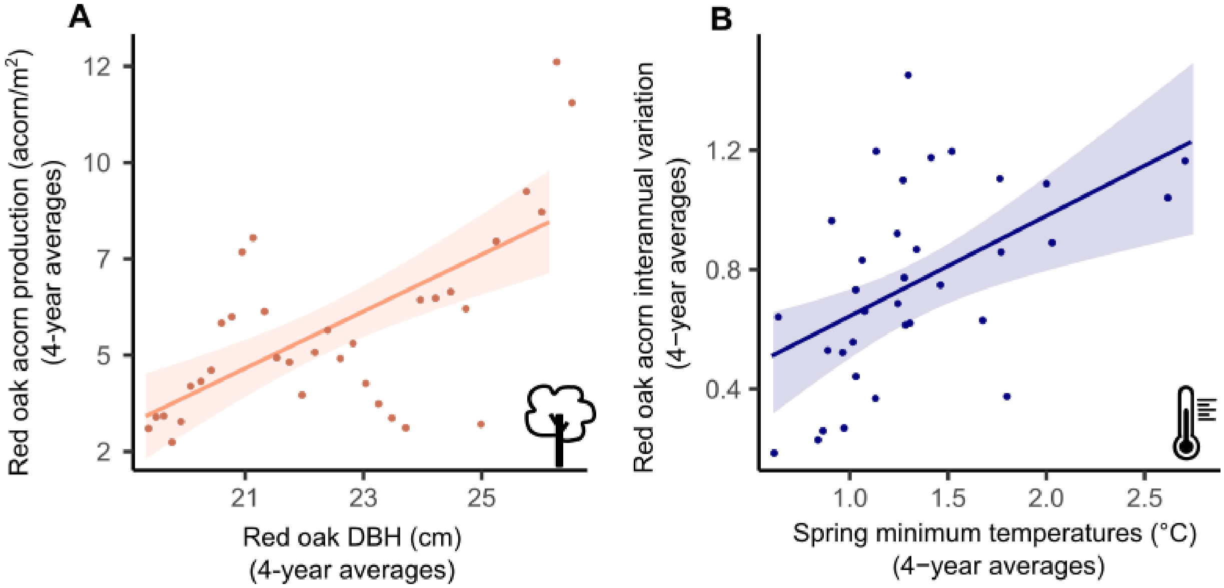

Fig. 5: Estimates of red oak acorn production and interannual variation (coefficient of variation) from the top-ranked regression models. **(A)** Red oak acorn production increased with tree growth represented by average annual DBH increment. **(B)** Red oak acorn interannual variation increased with spring minimum temperatures. Variables were measured annually but were included in the models as averages on a moving 4-year window. Response variables were log-transformed in the models and back-transformed for plotting. Ribbons in the figure indicate 95% confidence intervals. Data were collected in the Holt Research Forest, Maine, USA, between 1983 and 2021, where 5,112 red oak trees and 2,190 acorns were sampled.

Coupled effects of forest growth and climate change on small mammal abundance and body weight: results of a 39-year field study

Supporting Information

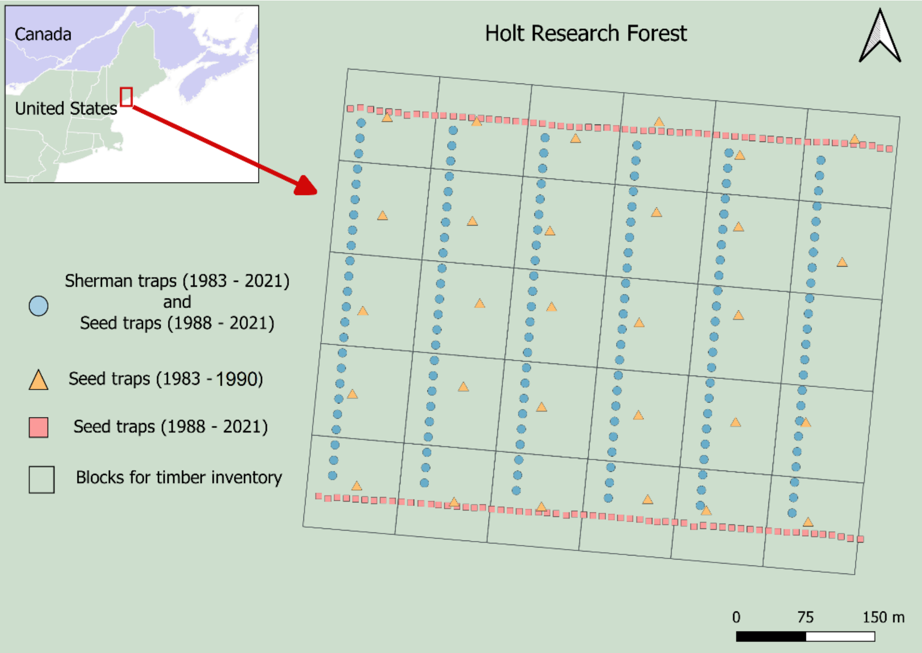

Fig S1: Study design in the Holt Research Forest (30-ha area located in Arrowsic, Maine, USA). Blue circles represent trap stations (n = 144) with two Sherman traps used to capture white-footed mice (*Peromyscus leucopus*) and one seed trap used to sample red oak acorns (*Quercus rubra*) (sample area = 0.042 m^2). These stations were distributed in six transect lines 100 m apart and were active between 1983 and 2021 (Sherman traps) and 1988 and 2021 (seed traps). Orange triangles represent seed traps (n = 29; sample area = 0.5 m^2) evenly distributed in the study area active between 1983 and 1990. Pink squares represent seed traps (n = 120; sample area = 0.042 m^2) placed in 10-m intervals along two east-west 600 m transects, active between 1988 and 2021. Rectangles represent 1-ha blocks (n = 30) used for red oak tree inventory in 1984, 1988, 1996, 2007, and 2020.

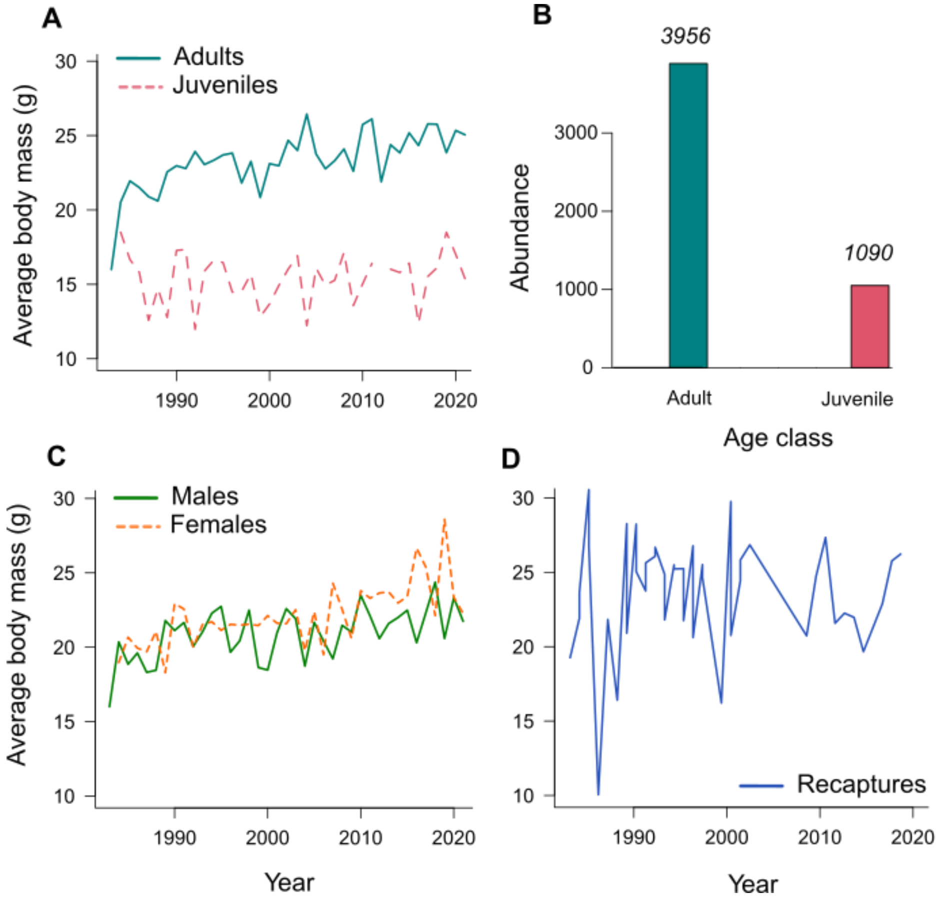

Fig S2: White-footed mouse (*Peromyscus leucopus*) trends in abundance between age groups, sex, and recaptured individuals. **(A)** Adults show an increase in body weight over time while juveniles have their weight stable. **(B)** Juveniles account for less than a third of the data. Numbers in italics indicate the sample size of each age category. **(C)** Both males and females are increasing body weight over time, suggesting that the increase cannot be explained by the increasing proportion of pregnant females at the time of trapping (August). **(D)** There is no temporal increase in the number of recaptures between years (i.e. individuals caught in two consecutive summers), suggesting that the increase in body weight cannot be fully explained by individuals getting older. Data were collected in the Holt Research Forest, Maine, USA, between 1983 and 2021.

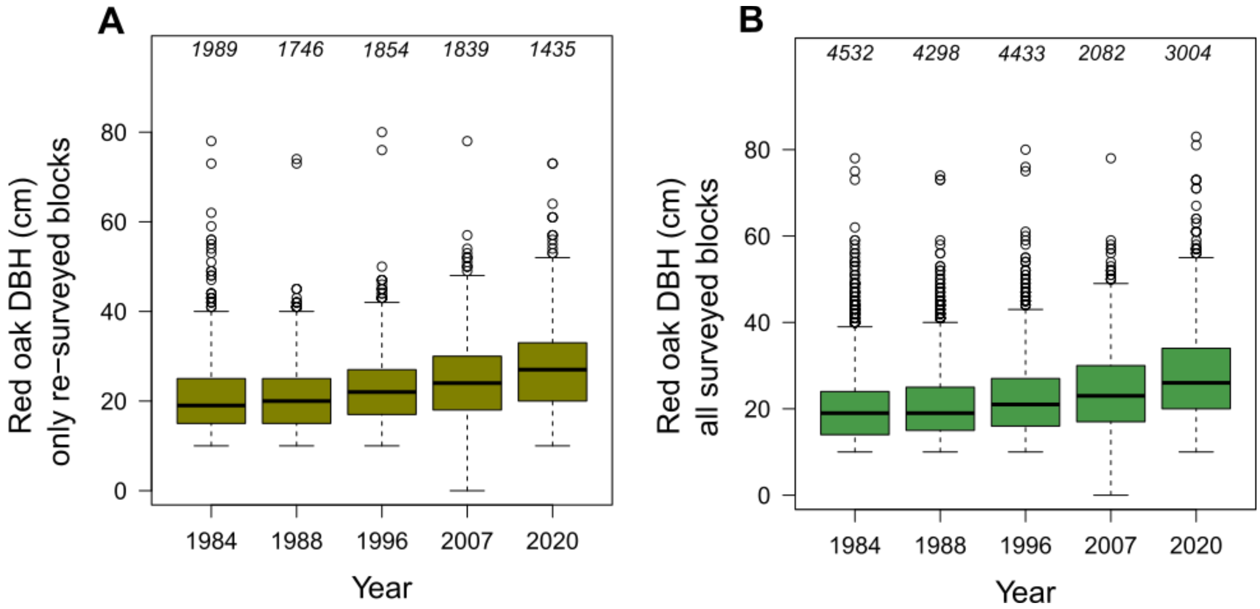

Fig. S3: Temporal trends of red oak trees' diameter at breast height (DBH). **(A)** Average DBH including only blocks that were surveyed all five years of inventory. **(B)** Average DBH of all blocks surveyed in each inventory. Numbers in italics indicate the sample size of each year. Data were collected in the Holt Research Forest, Maine, USA.

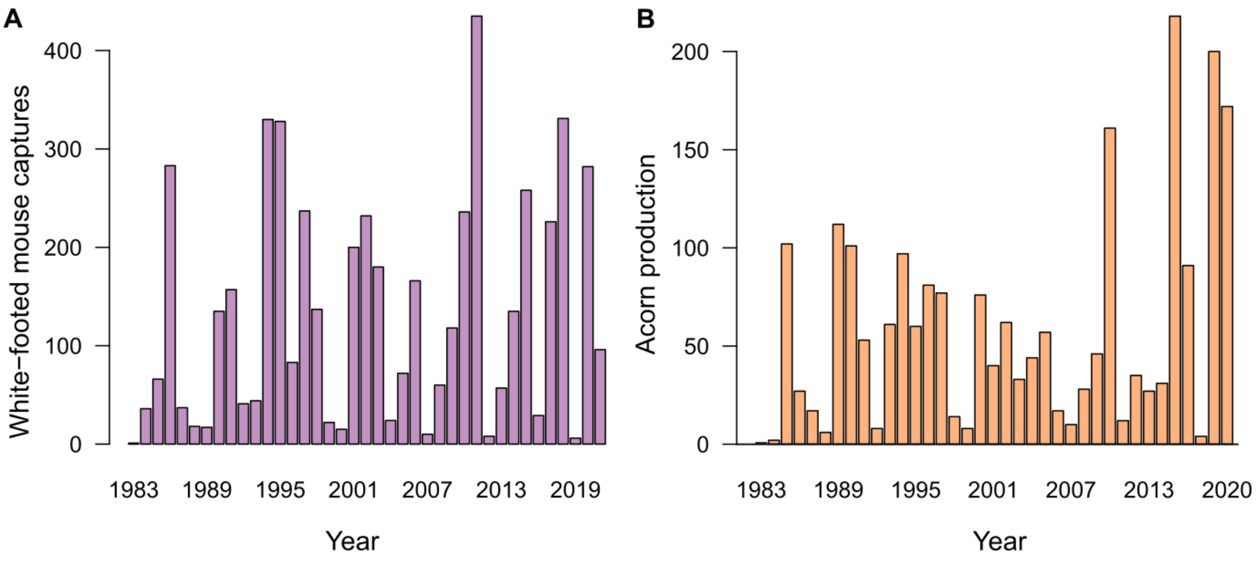

Fig. S4: Temporal trends of **(A)** white-footed mouse abundance (number of unique individuals caught per year) and **(B)** red oak acorn production (sum of acorns collected in all seed traps). Data were collected in the Holt Research Forest, Maine, USA, between 1983 and 2021.

Table S1: Top-ranking regression models for red oak (*Quercus rubra*) acorn production and interannual variation using a 10-year window with 1-year step. Only models within 5ΔAIC from the top model are shown. Acorn = red oak acorn production, time = number of time windows, DBH = red oak tree DBH, spring temp = spring minimum temperatures; winter temp = winter minimum temperatures; annual temp = annual minimum temperatures; k = number of parameters, ΔAICc = Delta Akaike Information Criterion; AICcWt = Akaike weight. Data were collected at the Holt Research Forest from 1983 to 2021.

Response	**Predictors**	**K**	**ΔAICc**	**AICcWt**	**p**	**R^2**
Acorn production	DBH	3	0.00	0.45	< 0.01	0.31
	time	3	0.74	0.31	< 0.01	0.29
	Winter temp	3	2.76	0.11	< 0.01	0.24
	Annual temp	3	2.90	0.11	< 0.01	0.23
Acorn interannual variation (CV)	Spring temp	3	0.00	0.99	< 0.01	0.50

Table S2: Regression models for white-footed mouse body weight and survival models using robust design with Huggin's estimator. Only models above 5ΔAIC from the null model (i.e. model without predictors) are shown. Acorn = red oak acorn production, time = number of time windows, fall temp = fall average minimum temperatures; annual temp = annual average minimum temperatures; winter temp = winter average minimum temperatures; k = number of parameters, ΔAICc = Delta Akaike Information Criterion; AICcWt = Akaike weight. Data were collected at the Holt Research Forest from 1983 to 2021.

Response	**Predictors**	**K**	**ΔAICc**	**AICcWt**	**p-value**	**R²**
Body weight	time + acorn	4	0.00	1	<0.001	0.85
	fall temp + acorn	4	10.77	0	<0.001	0.79
	time	3	16.08	0	<0.001	0.75
	acorn	3	32.10	0	<0.001	0.60
	fall temp	3	40.41	0	< 0.001	0.49
	annual temp	3	42.73	0	<0.001	0.45
	winter temp	3	54.56	0	0.001	0.22
Survival	body mass * time	7	0.00	0.70		
	body mass	5	2.41	0.22		
	abundance * time	7	41.61	0.00		

Table S3: Abundance (number of unique individuals) and average weight (in grams) of adult females between 2016 and 2021 at the Holt Research Forest, Maine, USA.

Year	Pregnant females		Non-pregnant females	
	Abundance	Average weight (g)	Abundance	Average weight (g)
2016	2	27.65	2	25.45
2017	53	27.27	22	25.33
2018	0	-	18	25.13
2019	0	-	0	-
2020	60	27.11	0	-
2021	11	26.9	0	-