



OPEN Integrating small mammal personality and population abundance into forest regeneration predictions for a managed, mixed species forest in Maine, USA

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Understanding forest regeneration is critical for predicting the future of forests, but most forest growth models overlook the animals responsible for driving regeneration dynamics. Scatter-hoarding small mammals are critical for the regeneration of many keystone plant species, and their personality influences their role in the seed dispersal process. Here, we take a first step toward integrating small mammal populations and personalities into forest regeneration predictions, building a modeling framework with empirical data where possible and identifying knowledge gaps. Our model predicts the number of cached eastern white pine (*Pinus strobus*) seeds under different personality and abundance scenarios for a deer mouse (*Peromyscus maniculatus*) population, parameterized with data from an eight-year field study conducted in Maine (USA). We demonstrate that white pine basal area growth is influenced by the personality distribution and abundance of a mouse population and specific forest management treatments. We recommend future research focusing on the knowledge gaps we identified and emphasize that our methods lay the groundwork for the collection and implementation of future empirical data needed for more robust forest growth models. Overall, due to the consequences of shifting personality distributions on white pine regeneration, we urge the conservation of behavioral diversity for maintaining healthy ecosystems.

Keywords Forest regeneration, Small mammal, Scatter-hoarding, Seed dispersal, Intraspecific variation

Forests cover almost one-third of the Earth's land surface, harbor the majority of terrestrial biodiversity, contain 662 billion tons of carbon, and contribute significantly to the global economy, making them an essential global resource¹. To predict the future of forests in the face of natural and anthropogenic disturbances² and for sustainable forest management³, we must understand natural forest regeneration and growth dynamics. Consequently, many models have been developed to predict forest dynamics and growth that take a variety of forms⁴. This includes empirically derived models like the Forest Vegetation Simulator (FVS^{5,6}) or SIMREG⁷ and forest gap or landscape-level models driven more by ecological principles and species functional traits (e.g.,^{3,8,9}). However, these models often ignore or greatly simplify regeneration processes due to their complexity and highly stochastic nature⁴.

In particular, these forest projection models generally overlook animal-mediated seed dispersal, a potentially critical process for forest regeneration. Animals disperse the seeds of more than half of plant species, influencing plant regeneration cycles, establishment, distribution, and survival^{10,11}. Scatter-hoarding by small mammals (i.e., storing seeds for later consumption in many dispersed caches¹²) is one important mechanism of animal-mediated seed dispersal present in forests worldwide^{12,13}. The regeneration of many dominant plant species depends on the activity of scatter-hoarding animals^{12,13}, therefore we must explore the consequences of small mammal scatter-hoarding behavior on forest regeneration to enhance our predictions of future forest composition and structure.

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The complexity of scatter-hoarders' relationship with dispersed seeds and the many decisions they make throughout the seed dispersal process make it complicated to quantify the impacts of scatter-hoarding on forest regeneration¹⁴, particularly because those decisions can vary from individual to individual¹⁵. Small mammals simultaneously play a mutualistic role with plant species, beneficially dispersing and caching some seeds, and an antagonistic role, eating and killing many seeds¹³. Whether rodents act mutualistically or antagonistically towards seeds depends on many factors, including small mammal personality¹⁶, and on many steps, or actions and decisions that small mammals must make with seeds. First, small mammals must find available seeds, then they must decide whether to consume or disperse seeds and, for dispersed seeds, how far to transport them and where to cache them^{17,18}. Finally, rates of cache recovery and pilferage (i.e., an animal other than the cache owner recovers seeds) are also important determinants of final seed fate¹⁹. Seeds which are consumed or taken down holes have little to no chances of germination²⁰. In contrast, seeds stored in shallow caches typical of rodent dispersers, and that escape pilferage and recovery, have higher chances of germination due to reduced desiccation and predation^{21,22}. Past research has explored these steps, assessing the effects of seed traits, abiotic conditions, predation and pilferage risk, rodent energetic state, and small mammal personality on seed fates^{15,17,18,23}. Further, estimates of seed germination and forest regeneration rates due to scatter-hoarding activity have been made^{14,24,25}, but while some steps of the process are well-studied, others remain poorly understood. Specifically, the compounding effects of small mammal personality on each step of the seed dispersal process, to ultimately determine to what extent personality influences forest regeneration, has not been assessed. Thus, work remains to examine each step in detail, the effects of personality on each step, and to link them together to quantify the number of seeds in a forest stand that may regenerate due to small mammal dispersal.

There has been recent research into the effects of personality on small mammal scatter-hoarding decisions^{15,16,26}, indicating the impacts of small mammal personality on forest regeneration. Specifically, Brehm et al.¹⁵ demonstrated that personality traits of deer mice (*Peromyscus maniculatus*), such as boldness and activity level, influence seed selection, dispersal distance, cache site selection, and the likelihood of seed consumption, ultimately affecting seed fate. Further, it has been found that deer mouse personality influences the likelihood of mutualistic seed outcomes, with more timid mice having more mutualistic interactions with white pine (*Pinus strobus*) seeds¹⁶. Thus, efforts to understand forest regeneration and subsequent changes in composition must consider not only small mammals' scatter-hoarding role but also their personalities to have a complete understanding of the factors influencing seed recruitment. However, to date, no attempt has been made to evaluate the potential effect of small mammal personality on forest regeneration by incorporating its influence on each step of the seed dispersal process. We envision the development of such models, incorporating small mammal abundances and personality distributions and the impacts of these attributes on their scatter-hoarding behavior to predict future forest composition and structure. However, some data gaps remain before a full version of such a model can exist.

To understand how distributions of personality within a small mammal population affect patterns of forest regeneration, a large-scale and long-term field study is necessary to quantify the personality of individual small mammals, track their space use, and record each interaction with a seed all the way through to either spring germination or consumption. Without such complete data, we take a first step toward the goal of integrating small mammal populations and their personalities into models of forest regeneration. We used empirical data where possible and made simplifications and assumptions where necessary, identifying knowledge gaps that must be filled for the complete development of such a model. We built a spatially explicit agent-based model that incorporates empirical data from an eight-year study in Maine, USA quantifying small mammal personality and seed dispersal to estimate the number of cached seeds in a forest stand depending on the abundance and personality distribution of the small mammal population (Fig. 1). We used the output from this model and the widely used Forest Vegetation Simulator (FVS;^{5,6}) to obtain the first estimates of the impacts of variation in small mammal personality on the regeneration of forests (Fig. 1). We used deer mice interactions with white pine seeds as our model system because deer mice are one of the most common scatter-hoarding rodents in our study system and were the most recorded rodents in field experiments. Additionally, white pine is the preferred food item for deer mice²⁷ and a common and commercially significant tree species in eastern North America. With our model we aimed to (1) evaluate the potential effects of small mammal personality on forest regeneration by assessing its influence on each step of the seed dispersal process and then projecting to the future under multiple scenarios of population abundance and personality and (2) identify key gaps in empirical research that we need to fill to fully parameterize such a model to evaluate how the personality distributions of small mammal populations alter forest growth.

Results

Over our eight-year study, we caught 1,177 deer mice ($n=3,402$ observations), with 1,025 deer mice having measures of time spent in the center of the open-field test ($n=1,656$ observations), which was significantly repeatable ($r=0.319$ [0.25–0.39]; Supplementary Table 1).

The models from the seed experiments, used to parameterize the agent-based model, included data from 25 deer mice ($n=343$ observations) for the probability of a mutualistic interaction with white pine seeds, 86 deer mice ($n=775$ observations) for the probability of pilfering a cache, 29 deer mice ($n=114$ observations) for the probability of transporting pilfered seeds, and 18 deer mice ($n=70$ observations) for the proportion of seeds mice found in a night.

There were 224 deer mice included in our population density scenarios of interest (i.e., minimum, average, maximum scenario for each grid). Of those, we calculated home ranges for 92 mice and used buffer home ranges (the size of the average home range calculated from 202 mice) for the remaining 132 mice.

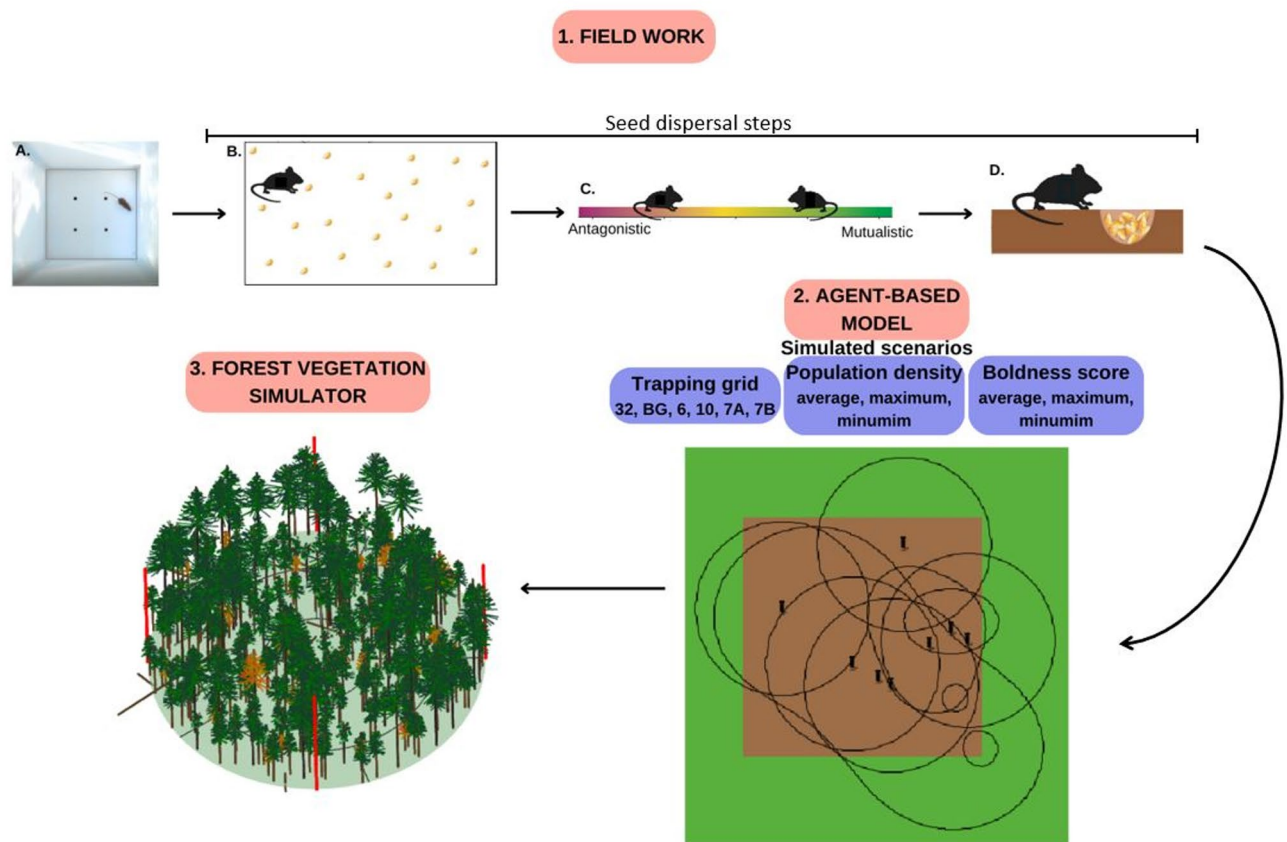


Fig. 1. Overview of our study. We (A) trapped and assayed the behavior (open-field test shown) of mice in the field. We also conducted three seed dispersal experiments evaluating (B) the proportion of seeds mice find in a night³⁵, (C) the probability of a mutualistic seed interaction by mice¹⁶, and (D) the probability of mice pilfering caches²⁶. We used this empirical data to parameterize 2.) an agent-based model in NetLogo⁵⁸ (trapping grid area of 0.81 hectare [ha] is shown in brown and mouse home ranges for one scenario are shown with black outlines) to predict the number of seeds cached in a forest stand based on the population density and personality of mice. Lastly, we used the output from this model and 3.) the empirically-derived, stand-level forest projection model, Forest Vegetation Simulator (FVS^{5,6}, to assess the effect of small mammal personality on forest regeneration and future structure/composition.

Agent-based model

More white pine seeds ended up cached at the end of the simulation when deer mice were all timid (i.e., minimum boldness score) than when they were all bold or had average boldness (Figs. 2A and 3). For instance, within one of our reference forest units (grid BG; 0.81 ha) with the population abundance held constant at the mean, when mice were timid, there was a 133.1% increase in seeds cached compared to when mice had the mean boldness score and a 190.03% increase compared to when mice had the maximum boldness score (Fig. 3C, Supplementary Table 2 Grid BG). Additionally, the most seeds were cached when the mouse population abundance was at the mean value (Figs. 2B and 3). Thus, when the boldness score was held constant at the mean in the same reference grid (grid BG; 0.81 ha), compared to the mean population abundance scenario, there was a 131.24% decrease in cached seeds when the population abundance was minimum and a 95.18% decrease when the population abundance was maximum (Fig. 3C). Personality and population abundance had similar effect sizes (beta parameter estimates for boldness: $\beta = -1.75$, $SE = 0.14$ and for population abundance squared: $\beta = -1.46$, $SE = 0.23$) on the number of seeds cached, with personality having a slightly stronger effect (Fig. 3). The strongest effect was forest management treatment, with the most seeds cached in irregular shelterwood forest units (Fig. 3A and B; see Supplementary Table 2 for the average predicted number of seeds cached for each scenario over 100 simulations reported with standard deviations).

Sensitivity analysis

Among all 6 trapping grids, the number of cached white pine seeds was sensitive to the boldness of the mouse population, with fewer seeds cached as boldness increased. The output was most sensitive to changes in boldness at low and moderate values of boldness but less sensitive to changes at higher values of boldness (Supplementary Fig. 1). The degree of sensitivity to boldness depended on forest treatment, with the irregular shelterwood forest units showing the greatest increase in the number of cached seeds as the boldness of the mouse population decreased (Supplementary Fig. 1; square points).

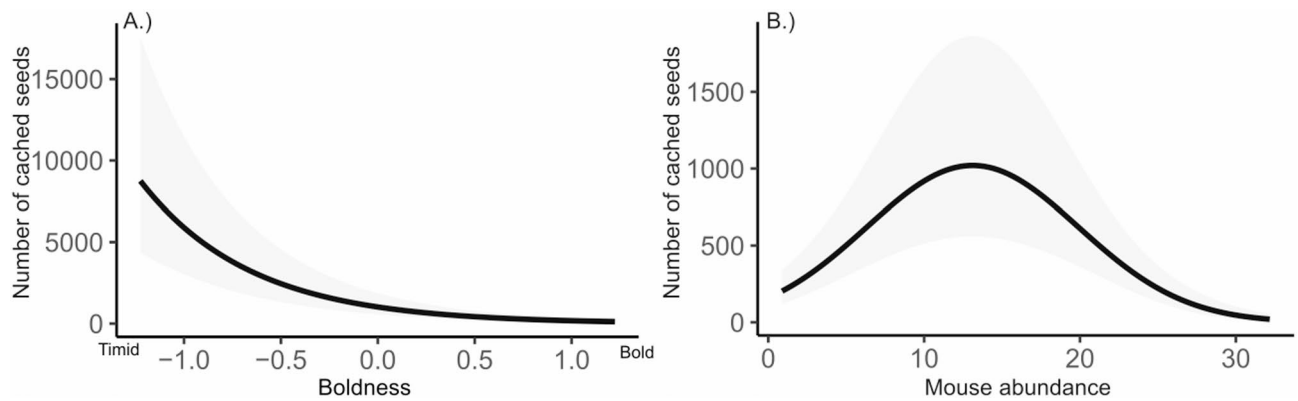


Fig. 2. The number of cached white pine seeds in a small mammal trapping grid (0.81 ha) at the end of simulations as a function of the (A) personality of the small mammal population and the (B) small mammal abundance over the same area (0.81 ha). The most seeds are cached and not pilfered (A) when small mammals are timid and (B) when there is an average small mammal abundance. Boldness is the BLUP value calculated for the proportion of time in the center of the open-field test for every mouse in the population and mouse abundance is the number of unique mice caught in a grid in a month. Plots are shown with all other variables held constant at the mean for the reference forest treatment and with 95% confidence intervals shown in gray.

Model parameter estimates: $\log(\text{Seeds cached}) \sim \text{Forest treatment (REF: } \beta = 0.54, \text{ SE} = 0.36, \text{ TWO: } \beta = 3.74, \text{ SE} = 0.35) + (\text{Population density})^2 (\beta = -1.46, \text{ SE} = 0.23) + \text{Boldness} (\beta = -1.75, \text{ SE} = 0.14) + \text{Home range overlap} (\beta = 0.32, \text{ SE} = 0.18) + \text{Intercept} (\beta = 6.39, \text{ SE} = 0.36) (R^2 = 0.87)$

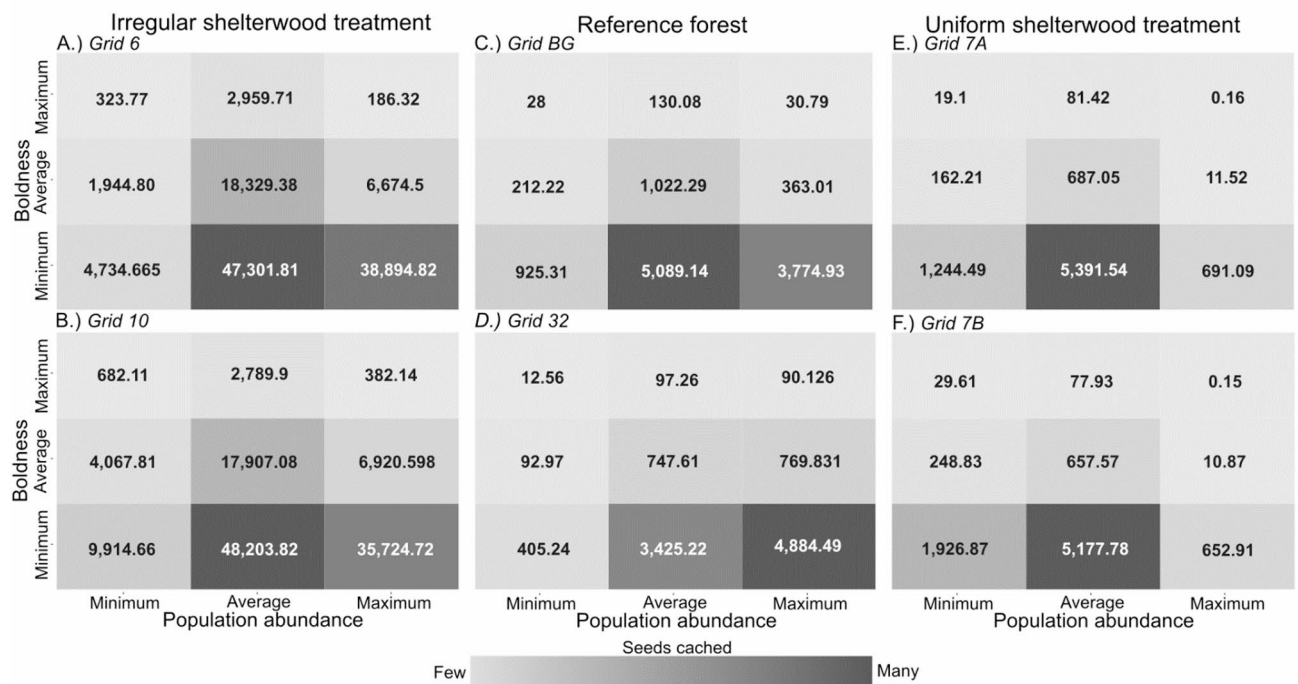


Fig. 3. The regression model showing the relationship between cached seeds and forest treatment, population density, boldness, and home range overlap with parameter beta estimates and standard error. Heatmaps display the predicted number of seeds cached within each small mammal trapping grid (0.81 ha) for each scenario of population density and personality averaged over 100 simulations. Panels (A) and (B) are grids 6 and 10, respectively, with irregular shelterwood treatment, panels (C) and (D) are grids BG and 32 in the reference forest, and panels (E) and (F) are grids 7A and 7B in the uniform shelterwood forest treatment. More white pine seeds are cached in the irregular shelterwood forest treatment, when mice are timid, and when population abundances are at the average value.

Additionally, in all grids, the number of cached seeds was sensitive to the number of movements mice made (i.e., the number of food patches they visited) within their home ranges, with more movements resulting in more cached seeds because more seeds were found (Supplementary Fig. 2). In the managed forest units, the number of cached seeds was only sensitive to the number of movements up to a point, after which all the seeds were already found and increasing movement had no effect on the number of cached seeds (Supplementary Fig. 2; square and triangular points). In the reference forest units, the number of cached seeds continued to increase with the number of foraging movements (Supplementary Fig. 2; circular points), likely due to the very low seed finding rates in these forests (Merz et al. *submitted*), which meant that even at high levels of mouse movement, not all the seeds were being found.

Forest vegetation simulator

White pine basal area increased the most from 2025 to 2075 for scenarios with timid mice and/or the mean population abundance (Fig. 4, Supplementary Table 3). For example, when holding the population density constant at the mean in one of our reference forest stands (grid BG), compared to when mice were timid, the white pine basal area in 2075 was 45.47% lower when mice had the average boldness score and 171.54% lower when mice had the maximum boldness score (Supplementary Table 3 Grid BG). Alternatively, when mice all had the mean boldness score, there was a 133.26% decrease in white pine basal area in 2075 when population abundance was at a minimum and an 89.87% decrease when population abundance was at the maximum compared to when the population abundance was at the mean value (Supplementary Table 3 Grid BG). See Supplementary Table 3 for all of the projected white pine basal area values and Supplementary Figs. 3–7 for visualizations of the growth in white pine basal area for each scenario we ran and in all trapping grids other than grid BG (displayed in Fig. 4). See Supplementary Table 4 for FVS outputs of stem density (trees per ha), total basal area, quadratic mean diameter, total volume, and total carbon for each scenario we ran and each decade we projected over.

Discussion

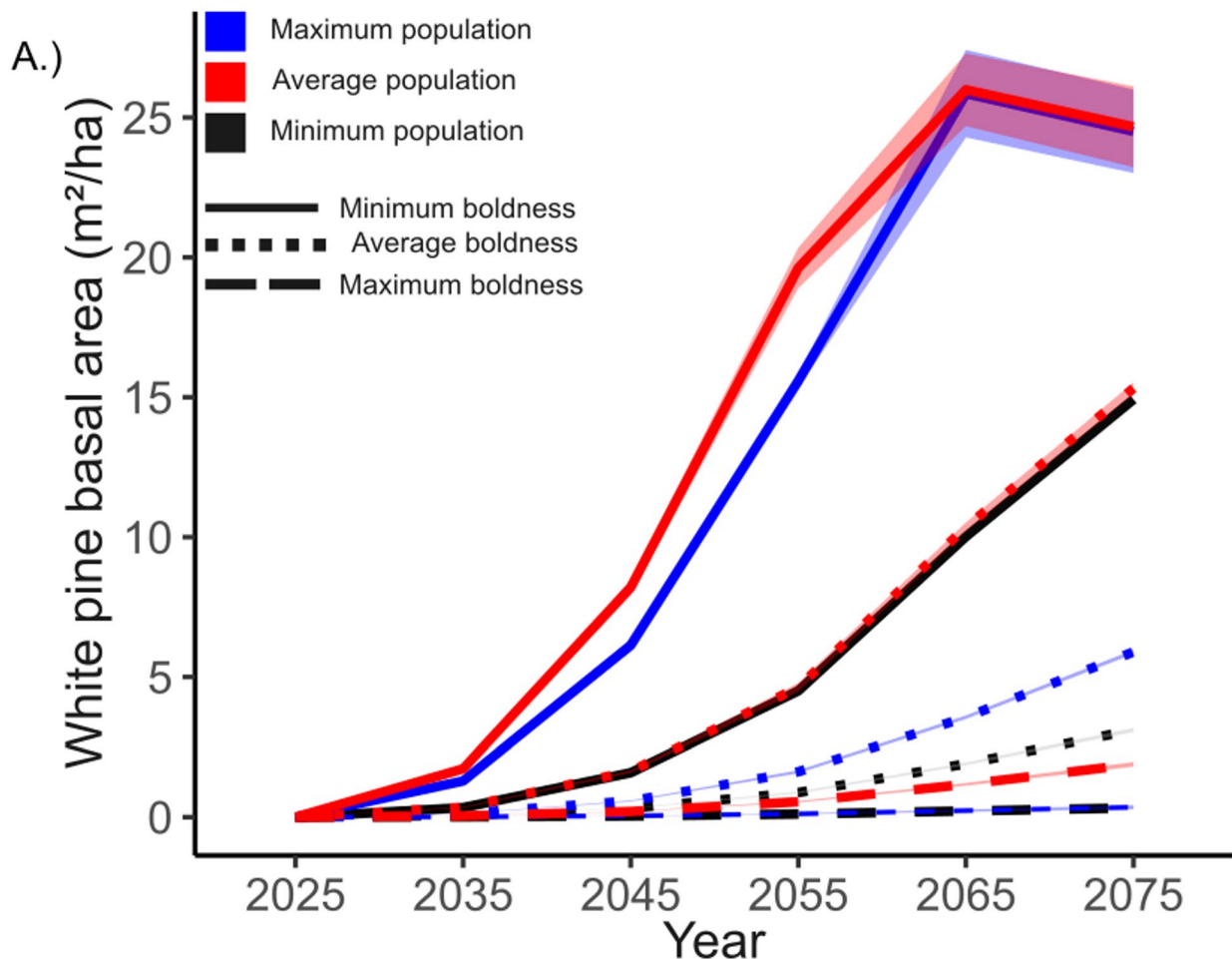
Through simulations of an agent-based model combining different population abundance and personality scenarios among a population of deer mice, we show that the personality distribution of a mouse population has consequences for the regeneration of white pine in a forest stand. Populations of timid mice resulted in the highest number of cached white pine seeds, leading to the greatest growth in white pine basal area projected over the next 50 years. Average small mammal abundances and irregular shelterwood forest units also resulted in increased seed caching. Additionally, we identified key steps in the seed dispersal process which are data deficient and recommend future work focuses on filling these gaps.

Factors influencing cache rate

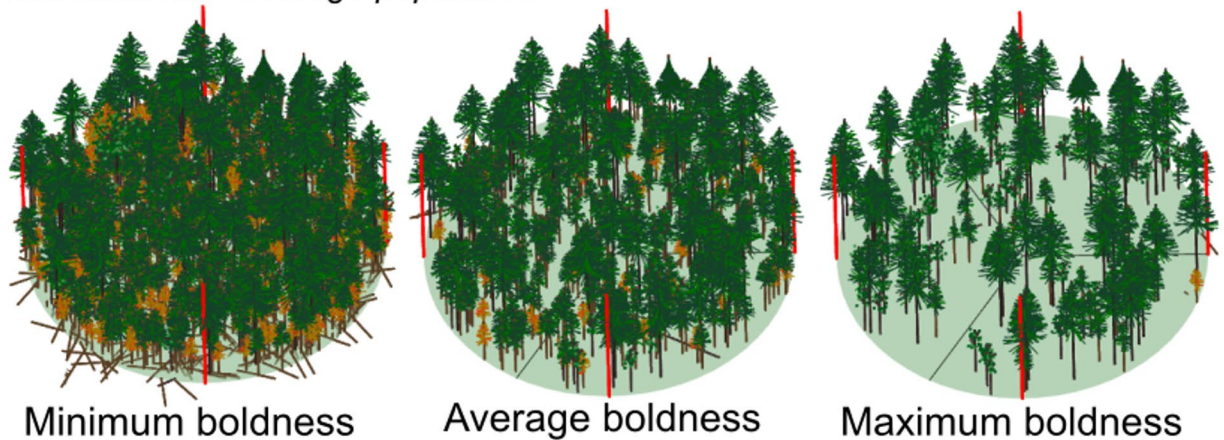
In our model, populations of timid mice resulted in higher numbers of cached white pine seeds than populations of mice with average or maximum boldness scores (Figs. 2 and 3). This was validated in our sensitivity analysis which illustrated that when all else was held constant, within each trapping grid as boldness increased, the number of cached white pine seeds decreased (Supplementary Fig. 1). These results are in line with findings from the experiment we used to parameterize our model, which found that bolder deer mice were more likely to interact antagonistically with white pine seeds, specifically being more likely to immediately consume seeds¹⁶. Consuming seeds takes more time than transporting them away, potentially putting animals at higher risk of predation while foraging²⁸, thus this result may be driven by the willingness of bolder mice to take the risk of immediate seed consumption while timid animals are finding more protected areas to either consume or cache seeds. Importantly, we found that the effects of boldness on small mammals' mutualistic tendency had tangible effects on the total number of seeds cached in a forest stand even when considered in combination with other steps of the seed caching process, such as seed finding and pilfering. Further, the difference in cached seeds due to personality had impacts on white pine regeneration, with forests with timid mice showing the greatest growth in white pine basal area over 50 years (Fig. 4).

Average mouse population densities also resulted in the most seeds cached (Figs. 2 and 3) and the most white pine basal area growth for most scenarios (Fig. 4) in our model. Higher population abundances resulted in more seeds being harvested, matching past work^{29,30}, and resulting in more seeds being cached, but high population abundances also led to increased population-level pilferage rates. Under the maximum population abundance scenario in our simulations, often every cache was pilfered, in line with previous work indicating high pilferage rates among scatter-hoarding mammals^{19,31,32}, specifically noting increased pilferage rates when small mammal abundances are higher³³. However, our recaching rate was often lower than reported among other scatter-hoarding rodents³⁴, but these results are for different small mammal and seed species and do not consider personality. We used the probability of a mutualistic interaction when mice initially interact with seeds (influenced by boldness¹⁶) to predict the probability of a positive interaction with seeds transported away after pilferage (40.27% of pilfered seeds²⁶). However, rates of mutualistic interactions may vary depending on whether it is with a harvested or a pilfered seed. Our use of the same probability of a mutualistic interaction for both scenarios is a limitation of our model due to a lack of data on the recaching probability of seeds pilfered by deer mice (Table 1). Further work should develop methods to track small seeds (such as white pine) dispersed by deer mice through multiple cache recovery and/or pilferage events to determine true recaching and ultimate survival rates of small seeds handled multiple times. Such methods exist for large seeds¹⁹ but we are not aware of any such methods for small seeds other than radioactive labeling³⁴, which poses health concerns.

Lastly, forest treatment also influenced white pine seed caching rates and thus regeneration, with the most seeds cached in irregular shelterwood forest treatments (Fig. 3). This is due to a combination of low seed harvesting



B.) Visualizations - average population



rates in reference forest units³⁵ and low seed caching probabilities in uniform shelterwood forest treatments¹⁶. Reference forest units are characterized by large cone-bearing trees and minimal understory growth, providing ample food resources but minimal cover from predation. Thus, reduced seed harvesting in these forests may be due to a surplus of seeds resulting in high rates of unfound and/or ignored seeds and increased predation risk limiting small mammal foraging activity. Uniform shelterwood forest units are characterized by dense stands of small trees, low-light conditions, and little understory cover, creating forests with limited food resources and high predation risk. This habitat may reduce caching, as small mammals may be more likely to immediately take seeds into holes under high-risk conditions. Although small mammals cache seeds in areas of high predation risk to reduce pilferage risk^{23,36}, when predation risk is uniformly high and food resources are limited, taking seeds down into holes may be preferred as the safest option to reduce both predation and pilferage risk. Irregular shelterwood forests are the most heterogeneous forests we worked within, providing sufficient cover and structure to mediate predation risk for mice while caching seeds. It is known that predation risk mediates the scatter-hoarding behavior of small mammals^{36,37}, thus the impact of forest treatment on caching rate may be due to varying levels of predation risk, but more research should be done to confirm this hypothesis.

◀**Fig. 4.** Results from the forest vegetation simulator (FVS^{5,6} illustrating the differences in the regeneration of white pine in a forest stand due to the different number of seeds cached by mice in each of these scenarios within one of our grids. (A) White pine basal area (m²/ha) predicted from 2025 to 2075 in one of our trapping grids for each scenario of population density and personality distribution. Estimates are shown with 95% confidence intervals displayed in the color corresponding to the line they are associated with, in instances where confidence intervals are not visible or hard to see, it is because they are very narrow. Basal area in 2075 is highest for scenarios with the least bold mice for both the minimum and average population densities. The scenarios with maximum boldness and both maximum and minimum population abundance have very similar data, thus the scenario for the maximum population abundance and maximum boldness is displayed with a smaller sized line so that both lines can be discerned (blue and black dashed lines). (B) Visualizations of the forest in 2075 for the average population density but for each of the different personality distributions. Results shown are for one of our trapping grids within the reference forest (grid BG), which was selected because it is from the reference, unmanaged forest and provides a useful visual example of the difference in white pine regeneration depending on mouse personality and abundance. See the Supplementary Materials Tables 3 and 4 for complete results of FVS outputs.

Knowledge gap	Assumptions of our model	Empirical work needed
Daily movement	Mice moved to 150 random patches within their home range	Radio telemetry tracking of nightly deer mouse movements to determine how much distance they cover, how many foraging bouts they make in a night, and spatial movement patterns
Cache recovery and pilferage	Cache recovery was not considered. Mice pilfered one time in our model, having access to each cache that was not their own	Tracking caches after initial seed dispersal and cache formation to determine cache recovery and pilferage rates through time
Recaching behavior	Mice had the opportunity to recache pilfered seeds one time using the probability of a positive interaction determined using data on deer mouse initial seed interaction and dispersal events	Tracking seeds through multiple cache recovery and/or pilferage events to either spring germination or consumption to determine the rates of recaching versus consumption and final seed fates
Germination and emergence rates of cached seeds	Germination was assumed to be constant at 66% ⁴²	Emergence experiments to assess the rates of germination and emergence of seeds handled and cached by deer mice and how those rates vary by cache site

Table 1. Table of the knowledge gaps we have identified in the seed dispersal process that would allow for a more complete parameterization of a future version of our model, the assumptions we used in our model to circumvent such gaps, and the recommended empirical work needed to truly fill those gaps.

Importantly, the seed finding experiment portion of this study was conducted during a white pine mast year (2023), which may have contributed to the relatively high level of unfound seeds we recorded during this experiment. Mice may have been satiated by the high amount of additional food resources outside of our study areas, leading to increased number of seeds left at our stations. Thus, our seed harvesting rates may be an underestimation when applied to non-mast years and future work should be done to generalize these results and determine how they may change under different scenarios of seed availability.

Limitations and future research

In the development of our model, we identified key steps in the seed dispersal process where data is lacking and further research is needed. To circumvent such gaps, we made some assumptions in the development of our model, but we provide recommendations for further research to help fill existing gaps and better parameterize a future version of our model. First, although data exists about the home range sizes of deer mice³⁸ and some limited data exists on deer mouse movement³⁹, comprehensive data about the movement patterns and activity levels of mice in a night are lacking. We assumed that all mice made the same number of foraging bouts and that mice could move anywhere within their home range between foraging bouts, allowing mice to move to 150 random patches within their home ranges (Table 1), although this is likely an unrealistic assumption. Our sensitivity analysis indicated the importance of this variable, as the number of cached seeds was sensitive to the number of movements mice made, with the number of cached seeds increasing with the number of patches mice visited up to a point, at which all seeds were found and increasing movement had no impact (Supplementary Fig. 2). Thus, we emphasize the importance of continued research into the movement patterns of mice as it does impact the number of seeds found and thus cached. High resolution radio telemetry data on individual mouse movements, particularly in complex mixed-deciduous forests, would enhance our model of mice foraging activity (Table 1).

Additionally, it is known that mice likely frequently recover their own caches^{40,41}, such as among other scatter-hoarding rodents³⁴, but very little is known about cache recovery rates of mice. We did not consider cache recovery in our model, but empirical work tracking individual mice, their caches, and cache recovery rates is critical work that would add to our model and allow the parameterization of this important part of the seed dispersal process (Table 1). Similarly, after cache recovery or pilferage events, seeds may be recached or consumed¹⁹, however rates of deer mouse recaching versus consumption after such events is unknown. Ultimately, tracking seeds through multiple recovery and/or pilferage and recaching events until either consumption or germination is necessary to better understand the final fates of seeds handled by small mammals (Table 1). Our model allowed mice to pilfer caches and used the probability of a mutualistic interaction calculated for deer mice interacting with seeds they

are harvesting¹⁶ to estimate recaching probability, however, further empirical data would allow a more realistic model of cache recovery, pilferage, and recaching rates (Table 1).

We also assumed a constant germination rate of 66%⁴² for all white pine seeds, but cache microsite impacts germination rates^{43,44}. Data on the real germination rates of seeds handled and cached in various locations by deer mice would be critical to better parameterize our model (Table 1). Given the current lack of information on how different cache sites affect cache survival and seed germination, we did not incorporate cache microsite information into our model. However, data on site selection by deer mice does exist¹⁵, and future versions of our model with better parameterized germination rates based on cache site could incorporate this information as well, adding another level of microhabitat complexity and realism to the model.

Finally, we focused on the effects of personality on seed caching rates due its importance for ecosystem services such as seed dispersal⁴⁵. However, there are many other factors that may influence seed caching rates among deer mice, such as body condition⁴⁶, environmental conditions (i.e., rainfall, soil moisture⁴⁷), or seed traits (i.e., size, perishability⁴⁸). Specifically, seed masting is a naturally occurring and likely significant factor that may impact small mammal behavior and seed caching rates⁴⁹. In the current study, assessing the impacts of seed masting on small mammal population abundances, personality distributions, and seed caching behaviors was outside the scope of the data we had and our focus on intraspecific variation. Thus, we used an average white pine seed abundance to simulate and make predictions for a non-masting year. However, future studies which collect detailed data on seed availability, mouse abundance, mouse personality distributions, and mouse seed caching behavior through time could look at how the relationships we found and predictions we made may change with changing seed availability and masting dynamics. Notably, with such data, our model could be adapted to look at the effects of other variables, such as seed availability, on small mammal seed caching rates. Additionally, we focused on white pine and deer mice, but complex interactions between multiple small mammal species influence the regeneration of many tree species and future iterations of our model with more data for other such species could incorporate this complexity. We also acknowledge the use of skewed cases of personality distributions (i.e., all timid versus all bold mice), which are likely oversimplified. However, we emphasize that we used these extreme cases to explore the scope of possible seed caching rates. Additionally, anthropogenic disturbances such as forest management and urbanization are known to shift the personality distributions of wild species^{15,50}, thus these seemingly extreme cases may be possible under future disturbance scenarios and should be considered to predict the effects of such personality shifts.

Conclusions

Overall, using an agent-based model parameterized with empirical data on mouse home range placement, foraging effectiveness, probability of a mutualistic interaction, and pilfering probability, we show that the personality distribution of a population of mice affects the regeneration of white pine trees. While further research is needed to fill some gaps in our model and get a complete picture of the consequences of small mammal personality on seed caching rates (Table 1), our methods are a first attempt to evaluate the potential effects of small mammal personality on forest regeneration by evaluating its influence on each step of the seed dispersal process. Due to the importance of scatter-hoarding animals for seed regeneration^{12,13} and the importance of animal personalities for ecosystem services⁴⁵, we foresee the continued development of such models which allow managers to consider small mammals and their personalities in predictions of forest regeneration. Specifically, models can be applied to inform our understanding of how forest ecosystems are changing and responding to environmental shifts, to identify tree species or forest areas which may need focused reforestation efforts versus those which have strong natural regeneration, and to understand the full consequences of management on forest regeneration. Forest management alters the personality distributions of mice and voles¹⁵, which, when taken together with our findings about how small mammal personality and abundance influenced seed caching differently in different forest treatments, indicates that forest management may be having unintended effects on regeneration. Using the known effects of forest management on small mammal personality and the fact that environmental heterogeneity and population density promote behavioral diversity⁵¹, it may be possible to predict the distribution of animal personalities in forest stands and to incorporate this information to understand cascading impacts of management on regeneration, better informing further management decisions and selection of forest treatments.

We emphasize the need for research focusing on the gaps we have identified for the complete parameterization of such models but hope that our methods can lay the groundwork for the eventual implementation of empirical data on small mammal seed dispersal for management decisions. Overall, due to the consequences of shifting personality distributions for the regeneration of white pine, we emphasize the need to conserve behavioral diversity for the maintenance of healthy and balanced ecosystems.

Methods

Below, we detail the methods of the empirical work used to parameterize our model. Here, we provide key information functional to this paper, while further details about specific methods can be found in Brehm et al.¹⁵, Merz et al.³⁵, Brehm and Mortelliti¹⁶, and Humphreys and Mortelliti²⁶ as referenced throughout.

Study area and small mammal trapping

We conducted a long-term small mammal capture-mark-recapture study from 2016 to 2023 in the Penobscot Experimental Forest (PEF) in Bradley and Eddington, Maine (USA). The PEF is located in the transitional zone between the eastern broadleaf and boreal forests and is composed of management units created by differing silvicultural treatments⁵². We established 90 × 90 m (0.81 ha) small mammal trapping grids within three different silvicultural treatments with two replicates of each, for a total of six grids. We worked within (1) reference forest

units (i.e., unlogged since the 1800s), which are mature forests with many large cone-bearing trees, (2) uniform (i.e., even-aged) shelterwood units, characterized by many small, densely-packed trees and low-light conditions, and (3) irregular (i.e., two-stage cut with reserves) shelterwood units, which have both dense areas with many small trees and some large cone-bearing trees scattered throughout⁵² (see the Supplementary Materials for more detailed descriptions of the silvicultural treatments, forest stands, and site conditions in units where we worked).

We trapped in each grid for three consecutive nights each month from June to October of each year. Grids were composed of 100 flagged trap sites spaced 10 m apart and we placed one Longworth trap bedded with poly fiber and baited with oats, freeze-dried mealworms, and sunflower seeds at each site. We checked traps in the morning and evening each night they were active. Over eight years, we had a total of 72,000 active trap nights.

Behavioral assays

We assayed the behavior of each captured small mammal with an emergence test for boldness and hesitancy⁵³, an open-field test for activity and exploration of a novel environment⁵³, and a handling bag test for docility⁵⁴. In this study, we only used data from one boldness behavior measured in the open-field test, which we describe below. For methods for the other tests and behavioral traits, see Brehm et al.¹⁵. For the open-field test, we placed animals into a clean 46 × 46 × 60 cm white box and recorded their behavior from above with a camera (Canon, Tokyo, Japan; PowerShot Elph 180 digital camera) for 5 min (Fig. 1A). After behavioral assays, we marked each animal with passive integrated transponders (Biomark PIT tags; MiniHPT8, 134.2 kHz), ear tags (National Band and Tag Co., Newport, Kentucky), and haircuts and recorded their weight, body and tail measurements, sex, age, and reproductive status. We then released each animal at their point of capture.

We analyzed open-field test videos using the software ANY-maze© (version 5.1; Stoelting Co., USA) to record the time individuals spent in the center of the arena as a measure of boldness. Lastly, we ran a repeatability analysis on the behavioral data and calculated a mean simulated best linear unbiased prediction⁵⁵ (BLUP) value for this behavior for each animal (see Supplementary Methods for full details of these analyses and calculations). We calculated the minimum, average, and maximum BLUP value of all mice from 2016 to 2023, obtaining three values to use in further analyses for timid, average, and bold mice populations, respectively.

Seed dispersal experiments

This study used empirical data from three seed experiments, which mimic the three key scatter-hoarding steps: (1) seed encounter (Fig. 1B), (2) seed predation or removal, dispersal, caching, and potential for germination (i.e., cached versus brought down a hole; Fig. 1C), and (3) possible pilferage (Fig. 1D). We briefly describe these experiments here and cite the original publications, which have fully detailed methods. From August to October 2023, we conducted an experiment to assess the foraging efficiency of small mammals³⁵. We created stations of high and low seed density, including both white pine and northern red oak (*Quercus rubra*), seeds, over a 0.91 m² area of the forest floor and monitored small mammal behavior at stations with trail cameras (Reconyx XR6 Ultrafire). We recorded small mammal identity, the time an individual arrived and left a station, timestamps for any seed they found, and which seeds they found, tracking availability of seeds throughout the night³⁵. We assessed small mammal effectiveness at finding seeds, running linear mixed-effect models with individual ID as a random effect and with the proportion of seeds found in a night (out of the amount available at an individual's first visit) as the response variable. The top model predicting the proportion of white pine seeds deer mice find at a station in a night included an effect of forest treatment³⁵.

In September and October of 2020, we performed an experiment to determine the likelihood of small mammals interacting mutualistically (i.e., removing and caching seeds or leaving seeds intact) or antagonistically (i.e., consuming seeds either at the site or after removal or taking seeds down a hole) with northern red oak, eastern white pine, and American beech (*Fagus grandifolia*) seeds¹⁶. We placed seeds in the field at stations monitored with trail cameras to record small mammal behavior, radio frequency identification (RFID) readers to identify small mammals by their PIT tags, and dusted with ultraviolet (UV) fluorescent powder (TechnoGlow) to allow tracking of removed seeds by following powder trails with a UV flashlight (uvBeast¹⁶). Thus, we identified small mammals with known personality and linked individuals to seed selection events and seed dispersal and final fate (i.e., at a cache, down a hole, or up a tree¹⁶). We then ran linear mixed-effect models with each seed interaction as an observation, whether it was mutualistic or antagonistic as the response variable, and individual ID as a random effect. The top-ranked model predicting the likelihood of deer mice mutualistically interacting with white pine seeds included boldness (i.e., proportion of time in the center of the open-field test), forest treatment, and body condition index¹⁶. For use in this study, we reran this top model using updated BLUP data, which was calculated including all mice from 2016 to 2023.

From July to October of 2022, we performed a pilfering experiment, creating artificial caches (i.e., 30 white pine seeds buried 0.5 cm in the soil) in each of our grids, monitored with trail cameras and RFID readers²⁶. We recorded the ID of visiting small mammals, whether they pilfered the cache, and whether they ate pilfered seeds at the cache or transported them away²⁶. We ran generalized linear mixed-effect models with individual ID as a random effect. The top model predicting whether deer mice will locate and pilfer a cache included body condition while the top model for whether mice would consume or transport seeds away was the null model²⁶.

Home range calculations

For our model, we were interested in the maximum, minimum, and average population density scenarios for each grid. Thus, we calculated the number of unique deer mice caught in each trapping grid in each month and determined which trapping month had the highest, lowest, and the value closest to the average number of unique mice for each grid. We generated a list of the mice caught in each of those months in the appropriate grid and, using the full capture data for each mouse, we calculated the home ranges for every individual included in those scenarios.

We used capture locations to calculate home ranges for deer mice included in these scenarios and caught more than four times using the *adehabitatHR* package⁵⁶ in R⁵⁷. We estimated kernel home ranges, using the 75% utilization distribution isopleth (*kernelUD* function). We also used the same method to calculate a home range for every deer mouse caught more than four times from 2016 to 2023 and calculated the average home range size for all deer mice. We then created buffer home ranges for mice that were included in our scenarios of interest but had four or fewer captures. We created circular home ranges the size of the average deer mouse home range and placed it in the weighted center of all trap sites for each individual. Thus, each grid had three full home range data sets, one for the scenario with the maximum number of unique mice captures, one for the minimum, and one for the average (closest real scenario to the average value; see Supplementary Fig. 8 for a visualization of the three population scenarios for one grid).

Agent-based model

We decided to use an agent-based model to assess the influence of small mammal personality on forest regeneration as it allowed us to explore the ecosystem-level consequences of many individual interactions between mice and white pine seeds. Thus, we built a spatially explicit agent-based model using NetLogo⁵⁸ to assess the consequences of abundance and personality of a small mammal population on the number of cached white pine seeds. We ran 100 simulations for every combination of trapping grid (6 grids), population density (minimum, average, maximum), and personality (minimum, average, maximum boldness) for a total of 54 combinations and 5400 simulations. For personality, every mouse in a simulation was assigned either the minimum, average, or maximum BLUP value for proportion time in the center of the open-field test.

Using the *gis* extension in NetLogo, we imported home range and trapping grid spatial data (Fig. 1) and ran each simulation over the area of one trapping grid (0.81 ha). We evenly distributed 205,559 white pine seeds (average white pine seed density across 0.81 ha from data collected in the Holt Research Forest; Arrowsic, Maine from 1988 to 2019⁵⁹, G. F. Dri, personal communication, June 2, 2023) across the patches within a trapping grid. Areas of mouse home ranges extending beyond trapping grids did not have white pine seeds, as we were considering this as outside of our study area. We created one mouse in the center of each home range and allowed them to move to 150 random patches within their home range. At each patch, we used the equation from Merz et al.³⁵ to parameterize the percent of available seeds that mice found (if there were 1 or fewer seeds, mice depleted the patch). Using the top-ranked model from Brehm and Mortelliti¹⁶, holding body condition index constant at the mean, we used the agent-based model to calculate the probability of each mouse positively interacting with found seeds, depending on forest treatment and personality. Thus, using the model, we calculated the number of seeds mice positively interacted with and how many of those positive interactions resulted in seeds left intact where they were found (29.41%¹⁶), removing those to get a count of how many seeds each mouse dispersed and cached intact (70.58% of seeds with a mutualistic interaction). Using the average number of white pine seeds per cache made by mice (24 seeds⁴⁰), we used the model to calculate the number of caches made by each mouse and the number of caches made total. Each mouse then had a probability of locating and pilfering available caches (including all caches minus those created by the mouse itself), parameterized using the top model from Humphreys and Mortelliti²⁶ while holding body condition index constant at the mean. Mice then transported away a proportion of pilfered seeds (40.27%²⁶) and seeds not transported away were considered consumed. We used the probability of a mutualistic interaction previously calculated for each mouse to calculate the number of pilfered and transported seeds each mouse recached and added them to the count of cached seeds. Ultimately, we used our agent-based model to calculate a total number of white pine seeds cached at the end of each simulation. See Supplementary Fig. 9 for a fully detailed workflow diagram.

We evaluated the impacts of population density, forest treatment, personality, and spatial overlap of home ranges on the number of seeds cached using linear regression models with the *lme4* package⁶⁰ in R⁵⁷. In NetLogo, we calculated an index of home range overlap, producing a count of the number of home ranges that overlap each patch in a grid and summing these values for a grid-level index for each scenario. We calculated the average number of cached seeds per scenario (over the 100 simulations). We then ran a linear model with the log transformation of the number of seeds cached as the response variable, forest treatment as a categorical predictor variable, personality, population density, and overlap index (all z-scaled) as numerical predictor variables, with a quadratic effect on population density.

Sensitivity analysis

To assess the degree to which changes in key input variables affected the output of our agent-based model, we ran a sensitivity analysis. We assessed the sensitivity of the predicted number of cached seeds to the boldness of the mouse population, as this was a variable of interest in this study, and to the estimated movement of mice in our model because this was a variable with very limited data and the value we selected (150 movements) was necessarily arbitrary. For boldness, we ran our agent-based model holding the population density constant at the mean but with 20 different values for boldness, ranging from the minimum to the maximum observed value and spaced evenly throughout our empirical data. For mouse movement, we ran the model with boldness and population density constant at the mean and changed the number of movements mice made, or the number of random patches they visited, per simulation. We assumed that our simulation took place over one month, or 30 nights, of mice activity, thus we included values for 1 movement per mouse per night (30 total), 5 movements per mouse per night (150 total), and 10–50 movements per mouse per night at intervals of 5 for a range of 30–1500 total movements per mouse per simulation. For both sensitivity analyses, we looked at each trapping grid separately and plotted our results with the input variable of interest versus the number of cached seeds to display the sensitivity of our output to our input variables.

Forest vegetation simulator

We used the Forest Vegetation Simulator (FVS^{5,6}; Northeast Variant; Version FS2025.1), a forest growth and yield model, because of its wide use as both a management tool and in research to project the development of forest stands⁶¹. We used this model to investigate the potential consequences of the observed differences in the number of cached seeds for the regeneration of forest stands. Although tree growth and forest regeneration after small mammal seed caching is independent of small mammal behavior, it is important to evaluate whether the differences in seeds cached by different small mammal populations have long-term consequences on forest structure and growth or whether those differences are equalized by other factors such as density-dependent mortality, resulting in the same number of surviving trees in years to come. Thus, we used the Forest Vegetation Simulator to model natural succession after cached seeds germinate to assess whether differences in numbers of cached seeds result in long-term differences in the forest or whether scenarios, despite different numbers of cached seeds, converge on similar long-term growth trajectories. We used a 66% white pine germination rate⁴² to calculate the number of seeds that may germinate for each scenario. Using tree inventory data from the management units we worked within in the PEF⁶² (see the Supplementary Materials for a description of the sampling protocols at the PEF and the tree inventory data we used), we modeled a shelterwood cut with a residual density of ~ 125 trees per ha (50 trees per acre) for each scenario in 2025 and then used the 'Planting and Natural Regeneration' tool within FVS to plant the appropriate number of germinated seedlings in 2026, assigning each of them a height of 1.3 m (4.5 ft) and a survival of 95%. We ran the simulation for 50 years, predicting white pine basal area out to 2075 (Fig. 1).

Data availability

Data and code used for all analyses in this manuscript are available on Figshare: <https://doi.org/10.6084/m9.figshare.29104274.v1>.

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References

1. FAO. The state of the world's forests 2022: forest pathways for green recovery and Building inclusive, resilient and sustainable economies. *Rome FAO*. <https://doi.org/10.4060/cb9360en> (2022).
2. Pretzsch, H. Forest Dynamics, Growth, and yield: A Review, analysis of the present State, and perspective. *Forest Dynamics, Growth and Yield: from Measurement To Model* https://doi.org/10.1007/978-3-540-88307-4_1 (Springer, 2008).
3. Shifley, S. R. et al. The past and future of modeling forest dynamics: from growth and yield curves to forest landscape models. *Landscape Ecol.* **32**, 1307–1325. <https://doi.org/10.1007/s10980-017-0540-9> (2017).
4. Weiskittel, A. R., Hann, D. W., Kershaw, J. A. Jr. & Vanclay, J. K. *Forest Growth and Yield Modeling* (Wiley, 2011).
5. Crookston, N. L. & Dixon, G. E. The forest vegetation simulator: a review of its structure, content, and applications. *Comput. Electron. Agric.* **49** (1), 60–80. <https://doi.org/10.1016/j.compag.2005.02.003> (2005).
6. Dixon, G. E. *Essential FVS: A user's guide to the Forest Vegetation Simulator. Internal Report 196* (USDA, Forest Service, Forest Management Service Center, 2002).
7. Perin, J. et al. SIMREG, a tree-level distance-independent model to simulate forest dynamics and management from National forest inventory (NFI) data. *Ecol. Model.* **440**, 109382. <https://doi.org/10.1016/j.ecolmodel.2020.109382> (2021).
8. Porté, A. & Bartelink, H. H. Modelling mixed forest growth: a review of models for forest management. *Ecol. Model.* **150**, 141–188. [https://doi.org/10.1016/S0304-3800\(01\)00476-8](https://doi.org/10.1016/S0304-3800(01)00476-8) (2002).
9. Wu, M. M. et al. A process-based framework for validating forest landscape modeling outcomes. *Environ. Model. Softw.* **185**, 106327. <https://doi.org/10.1016/j.envsoft.2025.106327> (2025).
10. Howe, H. F. & Smallwood, J. Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* **13**, 201–228. <https://doi.org/10.1146/annurev.es.13.1.10182.001221> (1982).
11. Rogers, H. S., Donoso, I., Traveset, A. & Fricke, E. C. Cascading impacts of seed disperser loss on plant communities and ecosystems. *Annu. Rev. Ecol. Syst.* **52**, 641–666. <https://doi.org/10.1146/annurev-ecolsys-012221-111742> (2021).
12. Vander Wall, S. B. *Food Hoarding in Animals* (The University of Chicago Press, 1990).
13. Gómez, J. M., Schupp, E. W. & Jordano, P. Synzoochory: the ecological and evolutionary relevance of a dual interaction. *Biol. Rev.* **94**, 874–902. <https://doi.org/10.1111/brv.12481> (2019).
14. Zwolak, R. & Crone, E. E. Quantifying the outcome of plant-granivore interactions. *Oikos* **121**, 20–27. <https://doi.org/10.1111/j.1600-0706.2011.19849.x> (2012).
15. Brehm, A. M., Mortelliti, A., Maynard, G. A. & Zydlewski, J. Land-use change and the ecological consequences of personality in small mammals. *Ecol. Lett.* **22**, 1387–1395. <https://doi.org/10.1111/ele.13324> (2019).
16. Brehm, A. M. & Mortelliti, A. Small mammal personalities generate context dependence in the seed dispersal mutualism. *PNAS* **119**, e2113870119. <https://doi.org/10.1073/pnas.2113870119> (2022).
17. Wang, B., Ye, C. X., Cannon, C. H. & Chen, J. Dissecting the decision-making process of scatter-hoarding rodents. *Oikos* **122**, 1027–1034. <https://doi.org/10.1111/j.1600-0706.2012.20823.x> (2013).
18. Wang, B. & Corlett, R. T. Scatter-hoarding rodents select different caching habitats for seeds with different traits. *Ecosphere* **8** (4), e01774. <https://doi.org/10.1002/ecs2.1774> (2017).
19. Jansen, P. A. et al. Thieving rodents as substitute dispersers of megafaunal seeds. *Proc. Natl. Acad. Sci.* **109**, 12610–12615. <https://doi.org/10.1073/pnas.1205184109> (2012).
20. Forget, P. M., Lambert, J. E., Hulme, P. E. & Vander Wall, S. B. *Seed Fate: predation, Dispersal and Seedling Establishment* (CABI, 2005).
21. Briggs, J. S., Vander Wall, S. B. & Jenkins, S. H. Forest rodents provide directed dispersal of Jeffrey pine seeds. *Ecology* **90** (3), 675–687. <https://doi.org/10.1890/07-0542.1> (2009).
22. Roth, J. K. & Vander Wall, S. B. Primary and secondary seed dispersal of Bush Chinquapin (Fagaceae) by scatter-hoarding rodents. *Ecology* **86**, 2428–2439. <https://doi.org/10.1890/04-0791> (2005).
23. Steele, M. A. et al. Do scatter hoarders trade off increased predation risks for lower rates of cache pilferage? *Behav. Ecol.* **25**, 206–215. <https://doi.org/10.1093/beheco/art107> (2014).
24. Kuprewicz, E. K. Scatter hoarding of seeds confers survival advantages and disadvantages to large-seeded tropical plants at different life stages. *PLOS One* **10** (5), e0124932. <https://doi.org/10.1371/journal.pone.0124932> (2015).
25. Wang, X., Zhang, L., Huo, X., Zhang, G. & Yu, F. Reduced rodent-mediated seed dispersal at forest edge hinders regeneration. *Global Ecol. Conserv.* **59**, e03571. <https://doi.org/10.1016/j.gecco.2025.e03571> (2025).

26. Humphreys, B. R. & Mortelliti, A. Pilfering personalities: effects of small mammal personality on cache pilferage. *J. Anim. Ecol.* **94** (3), 291–302. <https://doi.org/10.1111/1365-2656.14059> (2024).
27. Boone, S. R. & Mortelliti, A. Small mammal tree seed selection in mixed forests of the Eastern United States. *For. Ecol. Manag.* **449**, 117487. <https://doi.org/10.1016/j.foreco.2019.117487> (2019).
28. Lima, S. L., Valone, T. J. & Caraco, T. Foraging-Efficiency-Predation-Risk Trade-Off in the grey squirrel. *Anim. Behav.* **33** (1), 155–165. [https://doi.org/10.1016/S0003-3472\(85\)80129-9](https://doi.org/10.1016/S0003-3472(85)80129-9) (1985).
29. Kuprewicz, E. K. Mammal abundances and seed traits control the seed dispersal and predation roles of terrestrial mammals in a Costa Rican forest. *Biotropica* **45** (3), 333–342. <https://doi.org/10.1111/btp.12014> (2013).
30. Yu, F. et al. High rodent abundance increases seed removal but decreases scatter-hoarding and seedling recruitment along an elevational gradient. *Integr. Zool.* **18** (5), 843–858. <https://doi.org/10.1111/1749-4877.12695> (2022).
31. Cao, L. et al. Risk of cache pilferage determines hoarding behavior of rodents and seed fate. *Behav. Ecol.* **29** (4), 984–991. <https://doi.org/10.1093/beheco/ary040> (2018).
32. Dittel, J. W., Perea, R. & Vander Wall, S. B. Reciprocal pilfering in a seed-caching rodent community: implications for species coexistence. *Behav. Ecol. Sociobiol.* **71**, 1–8. <https://doi.org/10.1007/s00265-017-2375-4> (2017).
33. Dittel, J. W. & Vander Wall, S. B. Effects of rodent abundance and richness on cache pilfering. *Integr. Zool.* **13** (3), 331–338. <https://doi.org/10.1111/1749-4877.12317> (2018).
34. Vander Wall, S. B. & Joyner, J. W. Recaching of Jeffrey pine (*Pinus jeffreyi*) seeds by yellow pine chipmunks (*Tamias amoenus*): potential effects on plant reproductive success. *Can. J. Zool.* **76** (1), 154–162. <https://doi.org/10.1139/z97-169> (1998).
35. Merz, M. R., Record, S. & Mortelliti, A. (submitted). Intraspecific variation among scatter-hoarding small mammals mediates seed finding rates. *Ecology*, submitted.
36. Steele, M. A. et al. Scatterhoarding rodents favor high predation risks for cache sites: the potential for predators to influence the seed dispersal process. *Integr. Zool.* **10** (3), 257–266. <https://doi.org/10.1111/1749-4877.12134> (2015).
37. Merz, M. R., Boone, S. R. & Mortelliti, A. Predation risk and personality influence seed predation and dispersal by a scatter-hoarding small mammal. *Ecosphere* **14** (1), e4377. <https://doi.org/10.1002/ecs2.4377> (2023).
38. Wood, B. A., Cao, L. & Dearing, M. D. Deer mouse (*Peromyscus maniculatus*) home-range size and fidelity in sage-steppe habitat. *Western North. Am. Naturalist* **70** (3), 345–354. <https://doi.org/10.3398/064.070.0307> (2010).
39. Douglass, R. J., Semmens, W. J., Mattock-Cooley, S. J. & Kuenzi, A. J. Deer mouse movements in peridomestic and sylvan settings in relation to sin Nombre virus antibody prevalence. *J. Wildl.* **42** (4), 813–818. <https://doi.org/10.7589/0090-3558-42.4.813> (2006).
40. Abbott, H. G. & Quink, T. F. Ecology of Eastern white pine seed caches made by small forest mammals. *Ecology* **51**, 271–278. <https://doi.org/10.2307/1933663> (1970).
41. Vander Wall, S. B., Thayer, T. C., Hodge, J. S., Beck, M. J. & Roth, J. K. Scatter-hoarding behavior of deer mice (*Peromyscus maniculatus*). *Western North. Am. Naturalist* **61** (1), 109–113 (2001).
42. Bonner, F. T. Cone storage and seed quality in Eastern white pine (*Pinus strobus* L.). *Tree Planter's Notes* **37**, 4 (1986).
43. Vander Wall, S. B. Cache site selection by chipmunks (*Tamias* spp.) and its influence on the effectiveness of seed dispersal in Jeffrey pine (*Pinus jeffreyi*). *Oecologia* **96**, 246–252. <https://doi.org/10.1007/BF00317738> (1993).
44. Zhang, H. M. et al. Rodent-favored cache sites do not favor seedling establishment of shade-intolerant wild apricot (*Prunus Armeniaca* Linn.) in Northern China. *Plant Ecol.* **214** (4), 531–543. <https://doi.org/10.1007/s11258-013-0187-9> (2013).
45. Mortelliti, A. The importance of animal behavior for ecosystem services. *Trends Ecol. Evol.* **38** (4), 320–323. <https://doi.org/10.1016/j.tree.2022.10.009> (2023).
46. Merz, M. R., Colombini, F. & Mortelliti, A. Over the limit: consequences of Gray squirrel personality on the shifting range limits of oak and hickory species. *Global Ecol. Conserv.* **59**, e03539. <https://doi.org/10.1016/j.gecco.2025.e03539> (2025).
47. Yi, X., Liu, G., Steele, M. A., Shen, Z. & Liu, C. Directed seed dispersal by a scatter-hoarding rodent: the effects of soil water content. *Anim. Behav.* **86** (4), 851–857. <https://doi.org/10.1016/j.anbehav.2013.07.028> (2013).
48. Wang, B. & Chen, J. Seed size, more than nutrient or tannin content, affects seed caching behavior of a common genus of old world rodents. *Ecology* **90** (11), 3023–3032. <https://doi.org/10.1890/08-2188.1> (2009).
49. Jansen, P. A., Bongers, F. & Hemerik, L. Seed mass and mast seeding enhance dispersal by a Neotropical scatter-hoarding rodent. *Ecol. Monogr.* **74** (4), 569–589. <https://doi.org/10.1890/03-4042> (2004).
50. Tranquillo, C. et al. Going urban: variation in personality traits of an invasive species along an urbanization gradient. *J. Mammal.* **105** (6), 1300–1308. <https://doi.org/10.1093/jmammal/gyae077> (2024).
51. Mortelliti, A. & Brehm, A. M. Environmental heterogeneity and population density affect the functional diversity of personality traits in small mammal populations. *Proc. R. Soc. B* **287** (2020), 20201713. <https://doi.org/10.1098/rspb.2020.1713> (2020).
52. Kenefic, L. S. & Brissette, J. C. History of the Penobscot Experimental Forest, 1950–2010. *Penobscot Experimental Forest: 60 Years of Research and Demonstration in Maine, 1950–2010*, 1–20. (2014).
53. Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlshaw, G. & Heinsohn, R. Animal personality: what are behavioural ecologists measuring? *Biol. Rev.* **88**, 465–475. <https://doi.org/10.1111/brv.12007> (2013).
54. Mella, V. S. A., Ward, A. J. W., Banks, P. B. & McArthur, C. Personality affects the foraging response of a mammalian herbivore to the dual costs of food and fear. *Oecologia* **177**, 293–303. <https://doi.org/10.1007/s00442-014-3110-8> (2015).
55. Dingemanse, N. J., Moiron, M., Araya-Ajoy, Y. G., Mouchet, A. & Abbey-Lee, R. N. Individual variation in age-dependent reproduction: fast explorers live fast but senesce young? *J. Anim. Ecol.* **89** (2), 601–613. <https://doi.org/10.1111/1365-2656.13122> (2020).
56. Calenge, C. & Fortmann-Roe, S. Package ‘adehabitatHR’: home range estimation. *R Package Version 0.4.21* <https://cran.r-project.org/web/packages/adehabitatHR/vignettes/adehabitatHR.pdf> (2023).
57. R Core Team. R: A language and environment for statistical computing. R: A foundation for statistical computing, Vienna, Austria. <https://www.R-project.org/> (2024).
58. Wilensky, U. NetLogo. Center for connected learning and computer-based modeling. <https://ccl.northwestern.edu/netlogo/> (Northwestern University, 1999).
59. Witham, J. W., Moore, E. H., Hunter, M. L. & Kimball, A. J. A long-term study of an oak pine forest ecosystem: techniques manual for the Holt Research Forest. *Maine Agric. Forest Exp. Station, Tech. Bull.* **153**. (1993).
60. Bates, D. M., Maechler, M., Bolker, B. M. & Walker, S. lme4: Linear mixed-effects models using Eigen and S4. <https://cran.r-project.org/web/packages/lme4/lme4.pdf> (2015).
61. Anderson, P., Battaglia, M., Johnson, M., Kabrick, J. & Shaw, J. Research applications of the forest vegetation simulator: Documentation and citation. *USDA, Forest Service, Forest Management Service Center* <https://www.fs.usda.gov/fmssc/ftp/fvs/docs/gtr/DocumentingResearchApplicFVS.pdf> (2020).
62. Kenefic, L. S. et al. Overstory tree and regeneration data from the silvicultural effects on composition, structure, and growth study at penobscot experimental forest. 3rd Edition. Fort Collins, CO: Forest Service Research Data Archive. <https://doi.org/10.2737/RDS-2012-0008-3> (2025).

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Author contributions

A.M and M.R.M conceived the study; A.M., A.M.B, B.R.H., and M.R.M collected the data; all authors analyzed the data; M.R.M wrote the main manuscript text; all authors reviewed and edited the manuscript.

Declarations

Competing interests

The authors declare no competing interests.

Ethics statement

All animal trapping, handling, and experimental research was conducted in accordance with protocols approved by the University of Maine's Institutional Animal Care and Use Committee (IACUC protocols A2015_11_02, A2018-11-02, and A2021-12-01).

Additional information

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1038/s41598-025-29879-2>.

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