

# Small mammal controls on the climate-driven range shift of woody plant species

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Climate change is resulting in shifts in species' ranges as species inhabit new climatically suitable areas. A key factor affecting range-shifts is the interaction with predators. Small mammals, being primary seed predators and dispersers in forest ecosystems, may play a major role in determining which plant species will successfully expand and the rate at which range-shifts will occur. Plants dispersing seeds beyond the species' current range limits will encounter seed predators to which these seeds are novel; however, empirical studies of seed predator–novel seed interactions are lacking. The aims of our study were to: 1) quantify seed selection by small mammals presented with 'novel' seeds; 2) quantify the post-selection fate of 'novel' seeds; and 3) identify seed traits that affect seed selection and post-selection seed fate.

We designed a field experiment exposing small mammal communities to novel seeds produced by plants expected to shift their ranges in response to climate change. We matched novel seeds with reference 'familiar' seeds and studied key steps defining interactions between small mammals and novel seeds.

We found that the probability of selection of a novel seed varied among species and was, at times, higher than the selection probability of familiar seeds. Key traits that affected seed selection and the distance a seed was dispersed for caching were shell hardness and seed mass. We also found that 33% of dispersed seeds were cached in optimal germination sites (e.g. within fallen logs and buried under the leaf litter mat). Through seed emergence trials we found that emergence was higher for larger seeds, suggesting that the role of small mammals may be modulated by emergence rates.

Our results suggest that the interaction between small mammals and novel seeds may have cascading effects on climate-induced plant range shifts and community composition.

Keywords: climate change, novel seeds, range expansion, seed dispersal, seed predation, small mammals

## Introduction

Global climate change, including warming temperatures and altered precipitation regimes, is shifting the geographic distribution of many species (Kelly and Goulden 2008). However, several non-climatic factors may play a major role in determining the magnitude and direction of range shifts. Non-climatic factors include abiotic influences such as connectivity, soil properties and disturbance, as well as biotic factors such as the interaction with other species (i.e. predators, competitors, vectors) which may act as biological controls or may facilitate expansion (Hillyer and Silman 2010, Brown and Vellend 2014, Alexander et al. 2015, Urli et al. 2016). The effect of non-climatic factors could potentially impede the range shifts of some plant species, while facilitating movement of others, resulting in accelerated expansion (Brown and Vellend 2014, Urli et al. 2016). For seed-bearing plants, rodents and birds play a major role in dispersal and ultimate range expansion (Dennis et al. 2007, Vander Wall 2010). Rodents, in particular, by consuming specific seeds and rejecting others, can alter tree species composition in forest stands and may harvest up to 100% of seeds available in their territory, thus significantly reducing recruitment rates of their preferred seeds (Steele et al. 2005, Lobo 2014).

As plant ranges expand, the first dispersing seeds will be faced with seed predators that may have not previously encountered that particular seed or fruiting structure. These could either be populations of a seed predator that are naïve to that seed, or it could be a new species of predator (i.e. if the first dispersers enter the lower range limit of the predator species, examples provided in Supplementary material Appendix 1). The way in which seed predators contend with the novel seed or fruit, and the way in which this interaction subsequently unfolds could have dramatic consequences on a plant species' successful establishment in the new ecosystem. The outcomes of interactions between expanding plant species and granivores are hard to predict without empirical evidence, because these will ultimately depend on the particular ecological conditions in the areas of expansion (Urli et al. 2016). As a consequence, we cannot assume interactions between species in areas of current co-occurrence will represent those taking place under novel conditions. This uncertainty is particularly true for rodents, where local populations can develop specific enzymes required to overcome plant defense mechanisms (Vander Wall 2010), and where seed selection and cache management strategies depend on the relative availability of different species (Lichti et al. 2017). Further, small mammal community structure (i.e. the abundance/dominance relationships among species) may vary with latitude and longitude, such that the cumulative impact on seeds may differ substantially between areas of sympatry and areas of expansion (Kent et al. 2011).

Robust, evidence-based climate adaptation management requires an understanding of which plant species will be facilitated and which will be impeded in their expansion by seed predators and dispersers. Current modelling efforts focusing

on climate-induced range expansion tend to ignore interspecific interactions (Alexander et al. 2015), particularly interactions between plants and seed predators, possibly because of the lack of empirical data. Previous studies have investigated the potential role of predators (Hillyer and Silman 2010, Urli et al. 2016) as well as the role of rodents on non-native plants (Shahid et al. 2009, Chiuffo et al. 2018, Wróbel and Zwolak 2019); however, we are not aware of studies focusing on climate change and small mammal seed predators. Further, the role of small mammals is especially critical with respect to range expansion because, in addition to being seed predators, small mammals also function as dispersers by caching seeds some distance away from the parent tree (Vander Wall 2010, Lichti et al. 2017), which could lead to accelerated expansion (Jansen et al. 2004).

An additional gap in our knowledge of climate-induced range expansion concerns the particular seed traits that may make them more or less successful in their expansion by altering the likelihood of being preyed upon or dispersed by small mammals. Life-history traits clearly affect plant species' range expansion (Hannah 2015), as well as seed predation and dispersal by small mammals (Vander Wall 2010, Wang et al. 2013, Gong et al. 2015); however, the link between these two processes remains relatively unexplored. Such knowledge will help modelers and managers to make more general predictions of the likely 'winners' and 'losers' in terms of the potential for successful range expansion.

Through this empirical study we aim to reduce these knowledge gaps by addressing the following objectives:

- 1) Quantify seed selection by small mammals presented with 'novel' seeds. Novel in this context refers to seeds the mammals have not encountered before, produced by woody plants expected to shift their ranges in the near future (Prasad et al. 2007). Specifically, through cafeteria-style trials we compare the response of small mammals to novel seeds with their response to familiar seeds (i.e. seeds from plants currently present in the study area).
- 2) Quantify the post-selection fate of 'novel' seeds. Specifically, we assess a) which seeds are immediately predated and which are cached, b) the distance at which seeds are cached, c) in what substrates the seeds are cached and d) the emergence rates of novel seeds.
- 3) Identify seed traits that affect the probability of selection and post-selection seed fate.

Our study was conducted in Maine (northeast USA), which has a striking convergence of woody plant species range limits, with ca 64 species reaching their northern limits within the state (Fig. 1). These limits are controlled primarily by sharp climate gradients, which are expected to shift as climate changes (Schauffler and Jacobson 2002, Prasad et al. 2007). The strongest convergence of range limits – representing the northern limits of southerly species – lies just south of Acadia National Park (Schauffler and Jacobson 2002), which is a key conservation area in the USA. The national park will be among the first areas to experience the climate-driven

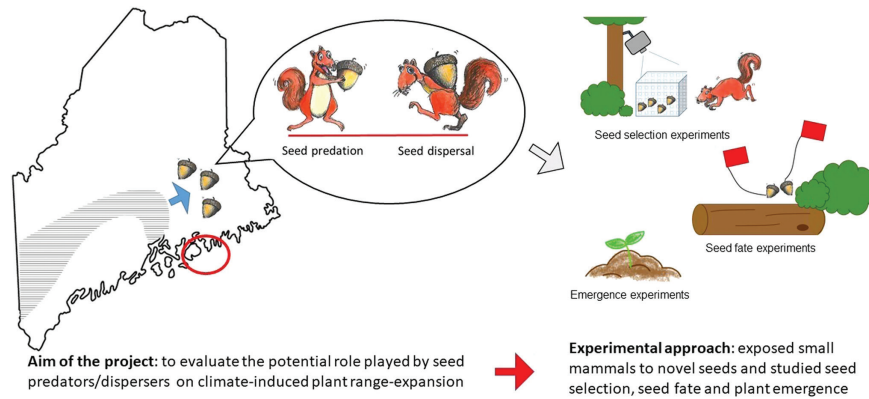


Figure 1. Conceptual overview of the project. The map on the left shows Maine (USA) and Acadia National Park (study area, circled in red) and the northern range limit of 64 woody plant species (the gray shaded area encompasses all range limits of the 64 species, redrawn from Schauffler and Jacobson 2002).

northward expansion of these woody plants, making this region ideal for studying the influence of small mammals on range expansions.

We performed a field experiment simulating the consequences of climate change effects by exposing small mammals to the seeds of 18 woody species predicted to expand in central Maine in the near future (Prasad et al. 2007). Further, we took advantage of recent improvements in the sensitivity and image quality of infra-red cameras, which provided an unprecedented opportunity to quantify, in a natural setting, the interaction between small mammal species and novel seeds (Fig. 1).

## Material and methods

### Study area

The study was conducted in Acadia National Park (Maine, USA). Vegetation in the park is dominated by the Acadian forest type, a diverse mixture of needleleaf and broadleaf trees. Predominant tree species include red spruce *Picea rubens*, balsam fir *Abies balsamea*, red maple *Acer rubrum*, red oak *Quercus rubra*, eastern white pine *Pinus strobus* and paper birch *Betula papyrifera*. The climate is damp and cool, with average annual temperatures of 8.3°C and mean precipitation of 144.0 cm year<sup>-1</sup>, which is evenly distributed throughout the year. We conducted our field experiments in 122 sites throughout Acadia National Park. The small mammal species present in the area that are included in our study are: American red squirrel *Tamiasciurus hudsonicus*, deer mouse *Peromyscus maniculatus*, white footed mouse *Peromyscus leucopus*, southern red backed vole *Myodes gapperi*, flying squirrels *Glaucomys volans* and *G. sabrinus* and the northern short-tailed shrew *Blarina brevicauda*.

### Target seeds

Target novel seeds were selected based on the likelihood of expansion in central Maine (Prasad et al. 2007). Given the

proximity of these southerly species' range limits (40–80 km depending on species), as well as clear evidence of recent climate change (Monahan and Fisichelli 2014), we consider their range expansion into Acadia National Park and surrounds to be likely in the near future. Among candidate seeds (listed in Table 1) we selected seven large seeds (e.g. oaks such as chestnut oak *Quercus prinus*, and hickories such as bitternut hickory *Carya cordiformis*), six medium-sized seeds (e.g. honeylocust *Gleditsia triacanthos* and blackgum *Nyssa sylvatica*), and five small seeds (e.g. rhododendron *Rhododendron maximum*, and eastern cottonwood *Populus deltoides*). Seeds were sourced both in the field and commercially and were microwaved prior to the experiments to prevent germination (except for the ones used in the emergence experiments) (Peters et al. 2004, Siepielski and Benkman 2008). Seeds were inspected for weevils prior to use and were kept at ~4°C overwinter.

### Experimental design

We conducted a series of cafeteria-style experiments in the field. Our 'treatment' seeds (i.e. novel seeds) were matched with 'reference' (i.e. familiar) seeds – seeds that are present in the study area and are thus expected to be known by small mammal populations inhabiting the park. These included a highly preferred seed (white pine *Pinus strobus*) and a less preferred seed (balsam fir, *Abies balsamea*). Small mammal preference for these seeds is well documented in the literature (Abbott and Hart 1960, Lobo 2014) and was also confirmed through a pilot study conducted in July 2017. For experiments involving large seeds, we also included a familiar oak species that is present in the area (red oak *Quercus rubra*) and consumed by small mammals. We acknowledge that an ideal experiment would have been to compare, through a matched pair design, between novel and familiar seed (e.g. each novel acorn would have been paired with a familiar acorn of very similar size, shape and nutritional content). This however is not possible because these matched pairs do not exist in our study system.

Table 1. Seed characteristics for the novel and reference seeds. Type of seed: N='novel', R='reference' seed. Group=group in which the seeds were deployed. Hardness follows the shore type D scale (range 0–100).

Common name	Scientific name	Type of seed	Group	Mass (g)	Hardness
White oak	<i>Quercus alba</i>	N	1, 2	5.169	29.3
Swamp oak	<i>Quercus bicolor</i>	N	1	2.671	19.2
Scarlet oak	<i>Quercus coccinea</i>	N	1	1.879	52.7
Chestnut oak	<i>Quercus prinus</i>	N	1, 2	8.657	21.7
Red oak	<i>Quercus rubra</i>	R	1, 2	3.262	35.2
Black oak	<i>Quercus veluti</i>	N	1, 2	1.875	22.4
Bitternut hickory	<i>Carya cordiformis</i>	N	2	4.618	48.1
Shagbark hickory	<i>Carya ovata</i>	N	2	6.627	80.3
Flowering dogwood	<i>Cornus florida</i>	N	3	0.11	87
Honeylocust	<i>Gleditsia triacanthos</i>	N	3	0.264	79.4
Spicebush	<i>Lindera benzoin</i>	N	3	0.1495	9.3
Blackgum	<i>Nyssa sylvatica</i>	N	3	0.1335	83.5
Sycamore	<i>Platanus occidentalis</i>	N	3	0.0001	1.8
Sassafras	<i>Sassafras albidum</i>	N	3	0.087	2.2
Sweet birch	<i>Betula lenta</i>	N	4	0.001	–
New Jersey tea	<i>Ceanothus americanus</i>	N	4	0.009	–
Mountain laurel	<i>Kalmia latifolia</i>	N	4	0.0001	–
Eastern cottonwood	<i>Populus deltoides</i>	N	4	0.001	–
Rhododendron	<i>Rhododendron maximum</i>	N	4	0.0001	–
White pine	<i>Pinus strobus</i>	R	1–4	0.017	–
Balsam fir	<i>Abies balsamea</i>	R	1–4	0.007	–

This study focuses on small mammals (rodents and shrews); therefore, to minimize visits by non-target species such as raccoons and birds, we offered seeds in small cups (diameter 6.5 cm and height 2.0 cm, maximum eight cups, see details below) placed within a mesh wire cage (sized 31 × 31 × 31 cm, mesh size 1 × 1 cm), with one cage at each site. The use of cups prevented wind from removing seeds. To increase stability, cups were attached to the cage by hook-and-loop fasteners. Each cage had two openings (sized 7 × 7 cm, one at each end) and was staked firmly to the ground. Cups were positioned in the side of the cage. To avoid any possible bias resulting from the positioning of seed cups, these were fastened along the inner edge of the cage, and the location of seeds was rotated such that each seed type was offered in all positions, and the neighboring cups were different in each site. Seeds were offered in equal quantities (i.e. the mass of seeds in each cup was the same) (Richardson et al. 2013, Berl et al. 2017). Cups were not replenished within an experiment, which was run for a maximum of three days (i.e. it terminated earlier if all seeds were consumed during the first two days). Experiments were conducted during September and October 2017 and May 2018. Both these periods represent times of natural availability of seeds (during the fall and soon after snow melting). Site locations were randomly selected within two areas of the Park, the Schoodic peninsula and the core area of Mt Desert Island. To minimize the chance of multiple visits across sites, these were spaced at least 100 m away from each other.

Seed choice and the interaction of individual small mammals with seeds were monitored through infrared Reconyx Hyperfire cameras mounted on trees and positioned at approximately 1 m height, with the main length of the camera parallel to the ground. Cameras recorded each visit to the

site (through a passive infrared motion detector) with a series of two-minute videos after each trigger. Each two minute-video is interrupted by two seconds (Supplementary material Appendix 1). The high resolution videos allowed us to quantify the type of seed selected and the availability of other seeds at each selection event. This approach allowed us to quantify true selection of seeds rather than just use (Manly et al. 2002, Richardson et al. 2013, Lichti et al. 2017). Selection reflects the actual preference of an animal whereas use reflects the mere utilization of a resource and does not necessarily reflect its preference. A resource is 'selected' if utilized disproportionate to its availability and 'used' if utilized in proportion to its availability (Manly et al. 2002). Quantifying selection allows researchers to identify the resources that are most important to an animal and provides valuable information on which tree species are the most likely to be impacted by small mammals. Before the development of high quality infrared cameras, performing true seed selection studies was complicated and, therefore, studies inferring seed selection are uncommon in the literature.

Additional variables recorded during video processing included the number of seeds selected and whether the seed was consumed on site or removed (binary variable).

Given the large number of seed species included in the experiment and differences in available quantities, we grouped offered seeds based on seed size (i.e. volume and mass), resulting in four distinct groups. All four groups included the same two familiar seeds (*Abies balsamea*, *Pinus strobus*), and two groups included *Quercus rubra* as a third familiar seed, allowing us to make comparisons among groups. Group one included all five species of oak acorns and the three familiar seeds (*Q. rubra*, *A. balsamea* and *P. strobus*); group two included two *Carya* species, three *Quercus* species (also used

in exp. one) and the three familiar seeds. The three novel *Quercus* acorns were retained to keep the overall number of seed species comparable to group 1. Group three included the five medium sized seeds and two familiar seeds (*P. strobus*, *A. balsamea*; group four included all small seeds and two familiar seeds (Table 1). Each of the four groups was used only once at a given site (with the exception of nine sites where we deployed group one and group three at least one week apart, starting with group one). Group one experiments were conducted in 30 sites, group two in 34 sites, group three in 43 sites and group four in 24 sites.

### Seed traits

Seed mass was measured on a sample of 20 seeds per species; however, for extremely small seeds we measured the number of seeds in a gram. Shell hardness was measured only on medium and large seeds using a Type D durometer using the Shore D hardness scale, which varies from 0 (medium hard) to 100 (extra hard). Nutritional traits, including protein, carbohydrate and lipid mass, were sourced from the literature or via lab analyses and are listed in Supplementary material Appendix 1 Table A1.

### Microhabitat variables

Previous studies have shown that the environmental context where an individual finds a seed may have strong effects on seed selection (Lichti et al. 2017, Pusenius et al. 2018). To account for environmental context, we measured a set of microhabitat covariates at each site. Covariates included the volume of coarse woody debris and the density of herbaceous, shrub cover and canopy cover. A full list of covariates and how they were measured is provided in Supplementary material Appendix 1 Table A2.

### Seed fate experiments

In addition to the seed choice experiments, we conducted a set of seed dispersal experiments to quantify seed fate in 61 sites (different from the seed choice experiments). Specifically, we were interested in determining whether a seed was consumed after removal from the experiment site, how far seeds were dispersed when cached, and on what substrates seeds were cached. We focused this experiment on the seven larger novel seeds (oak acorns and hickory nuts, which were offered simultaneously in each of the 61 sites), as we were not able to successfully apply and retrieve tags on the smaller species.

Each seed was fitted with a small tag including an ultra-thin wire (0.5 mm) passing through the seed and a reflective label to facilitate retrieval. Each label contained a unique code allowing it to be matched to a specific removal event (obtained via infrared cameras). Previous studies have shown that similar tagging methods have little effect on the decision by small mammals to disperse seeds (Xiao et al. 2006, Kempter et al. 2018); as all seeds were tagged using this method, we assume any influence to be negligible.

To avoid possible entanglement of the seed wire with the cages, seeds were offered on open ground. Two days following deployment, we searched for tags during the day (first) and when necessary at night using a flashlight. We searched for tags through a systematic search over a grid surrounding the site, up to 50 m from the site (Moore and Swihart 2008). When a tag was retrieved, we recorded if the seed had been consumed, the distance in meters to the source site, and the type of cache substrate (three categories: 1 = found on the surface of the forest floor, 2 = buried under the litter mat, under moss or coarse woody debris and 3 = found on a tree). Only non-consumed seeds were used for the calculation of dispersal distance.

We emphasize that dispersal distance should be considered a conservative estimate, as the likelihood of retrieval diminished with increasing distance from the source. We also acknowledge that the probability of retrieving a seed may be influenced by cache location, given that some locations (e.g. inside tunnels, high within a tree) confound detection and retrieval.

### Seedling emergence experiments

We assessed the ability of both the novel and familiar species to establish from seed within seed predator exclosures located on the Schoodic Institute campus within Acadia National Park. We conducted these experiments separately from the predation and dispersal experiments to minimize the risk of facilitating the colonization of these species. This part of the study included four 1 × 1 m plots with each subdivided into twenty-five 20 × 20 cm subplots. Each species was assigned to one or two subplots per plot and 5 or 50 seeds planted in each subplot, depending on seed size (e.g. only five oak acorns per subplot and 50 seeds of the small seeded species). A total of 1810 seeds were planted. Seeds were cold and moisture stratified during the winter prior to sowing based on species-specific requirements (details provided in Supplementary material Appendix 1 Table A3 (Bonner and Karrfalt 2008)). After planting, plots were sampled weekly throughout the growing season (May–September 2018) to determine the percentage of seedlings emerging (emergence is defined as the epicotyl breaking the soil surface).

### Data analysis

#### Seed selection

Seed selection data were analyzed using multinomial mixed-effects models, which are commonly used to quantify animal behavior (Koster and McElreath 2017) and food or habitat selection (Manly et al. 2002, Richardson et al. 2013) when dealing with categorical dependent variables. The dependent variable in these models is the seed choice (e.g. *Q. rubra*) made by an individual while visiting the cage. We used site as random effect to account for the potential lack of dependence of choice events made in the same site (i.e. a site could be visited more than once by the same individual) and we included the availability of all seeds (one variable per seed

species) as predictor variables in each model (Manly et al. 2002, Richardson et al. 2013). Analyses were conducted separately for each of our four groups (we used *A. balsamea* as our reference category in all analyses (Koster and McElreath 2017)). Because our focus here is the cumulative effects of the small mammal community as a whole, we combined data from all small mammals.

Multinomial mixed effects models were fitted and plotted using Rstan (interface to software Stan) and rethinking packages for R. Rstan uses Hamiltonian Monte Carlo methods for parameter estimation, a preferred method for complex models. To facilitate good mixing of the Hamiltonian Monte Carlo chains, we provided weakly informative priors for the fixed effect parameters and variance–covariance matrices (McElreath 2015, Koster and McElreath 2017). For all models we used three chains of 2000 iterations (including 1000 warm-up iterations) (McElreath 2015, Koster and McElreath 2017). We evaluated model convergence and adequate mixing by inspecting traceplots and checking the number of effective samples ( $n_{\text{eff}} \sim$  actual number of iterations) and the Gelman–Rubin convergence diagnostic ( $R_{\text{hat}} < 1.1$ ) (McElreath 2015). We started by fitting a model including site as random effect and the seed availability covariates as fixed effects (i.e. the availability of each seed type, sensu (Manly et al. 2002, Richardson et al. 2013)). We then sequentially added additional fixed effects, which included season (fall versus spring) and microhabitat variables (Supplementary material Appendix 1 Table A2). Models were compared using the widely applicable information criterion (WAIC), and for models within two delta WAIC, we tested for additive effects among covariates. As pointed out by Koster and McElreath (2017), when dealing with multinomial multilevel models, interpretation of coefficients is not straightforward and may be misleading; therefore, we based our inference on the final probability of selection and its 89% percentile intervals (Koster and McElreath 2017, see McElreath 2015 for a discussion on 89% versus 95% percentile intervals).

The final probability of selection of each seed was calculated considering 100% availability of each of the other seeds (i.e. the probability of choice when each seed species is available in equal weight).

### **Traits affecting seed selection**

To investigate which seed traits were most likely to affect seed selection, we calculated the difference between the probability of selection for the given seed and the probability of selection for *A. balsamea* (our ‘low selection’ familiar seed and also reference category in the multinomial analyses). In this way we were able to standardize our results across experiments. Data were analyzed by fitting mixed-effects models using the difference with *A. balsamea* as response variable and trait data as predictors (Zuur et al. 2009). We used ‘group’ (Table 1) as a random effect to account for potential dependence between results originating from the same group. As nutritional values of seeds were correlated among each other, which is a well-known pattern for seed nutritional traits (Lichti et al. 2017),

we did not fit additive models with correlated variables. We compared models through the Akaike information criteria corrected for small sample sizes (AICc) and obtained predictions through model averaging using top ranking models within two delta AICc (Burnham and Anderson 2002). We excluded the two familiar seeds (*P. strobus* and *A. balsamea*) from this analysis. We take the dependences among traits into account in our interpretation of results.

### **Seed predation versus removal (seed selection experiments)**

The infra-red videos were detailed enough to allow us to quantify whether a seed was consumed at the experimental site (i.e. in the cage) or removed for later consumption, which could include consumption in the immediate surroundings of the site. Data were analyzed by fitting mixed-effects models with a binary logistic response variable (consumed within the cage versus removed) using glmer function in R. We used site as a random effect, whereas fixed effects included season, seed species, small mammal species and microhabitat variables. Models were ranked and compared by using the AICc and predictions were obtained through model averaging. Models were fit using lme4 package for R.

### **Seed predation versus caching (dispersal experiments)**

Seed-fate data for the tagged seeds (acorns and hickories only) were also analyzed by fitting mixed-effects models with a binary logistic response variable (seed retrieved consumed versus seed retrieved intact) using site as random effect and seed species as fixed effect. Models were fit using lme4 package for R.

### **Dispersal distance**

Dispersal–distance data for all species pooled were analyzed by fitting mixed effects models with distance in meters as the response variable. We used site as a random effect to account for repeated observations within a site and used seed trait data as predictors (Zuur et al. 2009). Models were ranked and compared by using AICc and predictions were obtained through model averaging. Models were fit using nlme package for R.

### **Cache site**

Due to relatively small sample sizes, cache data were pooled across seed species and analyzed through a  $\chi^2$ -test.

### **Seed emergence**

Our analyses with the seed emergence data focused on establishing a relationship between emergence and seed size. Data were analyzed through a mixed-effects binomial regression with emergence success as response variable (binary variable: emerged versus not-emerged), seed mass as predictor, and cell nested within plot as the random effect using the lme4 package for R. We also report the spearman rank correlation coefficient between seed mass and emergence success.

## Data deposition

Data are available from the Figshare Digital Repository: doi: 10.6084/m9.figshare.8938007 (Mortelliti et al. 2019).

## Results

Through infra-red cameras we recorded a total of 1686 seed-selection observations (851 *Tamiasciurus hudsonicus*, 367 *Peromyscus* spp., 309 *Myodes gapperi*, 121 *Glaucomys* spp. and 38 observations from shrews and other species).

### Seed selection

#### Group 1 (acorns)

The top-ranked model in the multinomial mixed effects analyses did not include any fixed effects apart from seed availability (Table 2). Predictions from this model (Fig. 2) show a group of seed species with a probability of selection slightly higher or comparable to the probability of selection for *Pinus strobus* and *Quercus rubra* (these include the novel species *Quercus bicolor*, *Q. coccinea* and *Q. velutina*). On the opposite end we find two species (*Quercus alba* and *Q. prinus*) with an extremely low probability of being selected compared to the three reference species.

#### Group 2 (acorn and hickories)

The top-ranked model in the multinomial mixed effects analyses for group 2 included only availability of each type of seed as fixed effects (Table 2). Predictions from the top-ranked model showed that the two hickories had opposing preference levels (Fig. 2), with *Carya ovata* being relatively high (i.e. comparable to top choice seeds) and *C. cordiformis* being low (i.e. preference levels lower than *A. balsamea* and comparable to *Q. prinus*). Results from oaks are in line with those from group 1.

Table 2. Seed selection. Results for the multinomial mixed-effects models with seed choice as categorical response variable. Model ranking according to  $\Delta$ WAIC (delta widely applicable information criterion); only models  $<2$   $\Delta$ WAIC are shown. Availability=availability of each type of seeds at any given point in time during the experiment, CWD=coarse woody debris volume, Shrubs=density of shrubs at 2.4m. Group 4 data were not analyzed through multinomial mixed-effects models, results are shown in Supplementary material Appendix 1 Fig. A1.

Model	$\Delta$ WAIC	Cumulative Akaike weights
Group 1		
Availability	0.000	0.333
Availability + season	0.482	0.261
Group 2		
Availability	0.000	0.416
Availability + CWD	0.713	0.291
Availability + Canopy cover	1.898	0.161
Group 3		
Availability + Shrubs	0.000	0.937

#### Group 3 (medium sized seeds)

The top-ranked model in the multinomial mixed effects analyses for group 3 included the availability of each type of seed as fixed effect and the cover of shrubs at 2–4m (Table 2). Predictions from the top-ranked model showed variable levels of preference among seeds (Fig. 2). The most preferred seed was *Nyssa sylvatica*, with probability of choice slightly higher than that of *P. strobus*. *Cornus florida*, *Gleditsia triacanthos* and *Sassafras albidum* had a similar levels of preference, which were lower than the selection probability for *A. balsamea*. Finally, the least preferred seeds were *Lindera benzoin* and *Platanus occidentalis*, both with percentile intervals lower than those of *A. balsamea*.

#### Group 4 (small seeds)

The total number of visits to sites with group 4 seeds was low (74 visits out of a total of 24 sites deployed), which precluded fitting multinomial mixed-effects models to these data. We report the proportion of seeds consumed within visited sites, showing that larger seeds had a substantially higher consumption rate (Supplementary material Appendix 1 Fig. A1). Specifically, *P. strobus* was the most consumed seed (67%) followed by *A. balsamea* (41%), *Populus deltoides* (6.5%), *Ceanothus americanus* (3.3%), *Rhododendron maximum* (3.2%), *Betula lenta* (2.6%) and *Kalmia latifolia* (0.3%).

#### Group 1–3 (red squirrel *T. hudsonicus* data removed)

To evaluate if the results were mostly driven by the most abundant species (the red squirrel) we removed these data and re-run the multinomial mixed effects analyses for group 1–3. The seed selection results are very similar (Supplementary material Appendix 1 Fig. A2) and the few noticeable differences (such as a lower probability of selection of *C. florida* in group 3) have 89% percentile intervals overlapping the estimates including red squirrel data (shown in Fig. 2).

#### Traits affecting seed choice

By fitting mixed-effects models predicting the probability of selection for each seed species (group 1–3 only), we found that the most preferred seeds (relative to *A. balsamea*) across the study were the ones with harder shells (top-ranked model) and the larger ones (second-ranked model within two delta AICc, Table 3; model predictions are shown in Fig. 3). The third-ranked model included a positive relationship with percentage carbohydrates.

#### Consumption versus removal (seed choice experiments)

The top-ranked models for mixed effects logistic regression (seed immediately consumed versus removed) are shown in Table 3. The probability of removal was significantly higher than the probability of predation for all seed species ( $p < 0.05$ ) with the exception of *P. strobus*, *P. occidentalis* and *C. ovata* ( $p > 0.5$ , beta values were positive in all three cases). Through the model we also found that the probability of removal was significantly higher in the fall than in the spring ( $p < 0.05$ ), and voles and shrews had a higher probability of removing

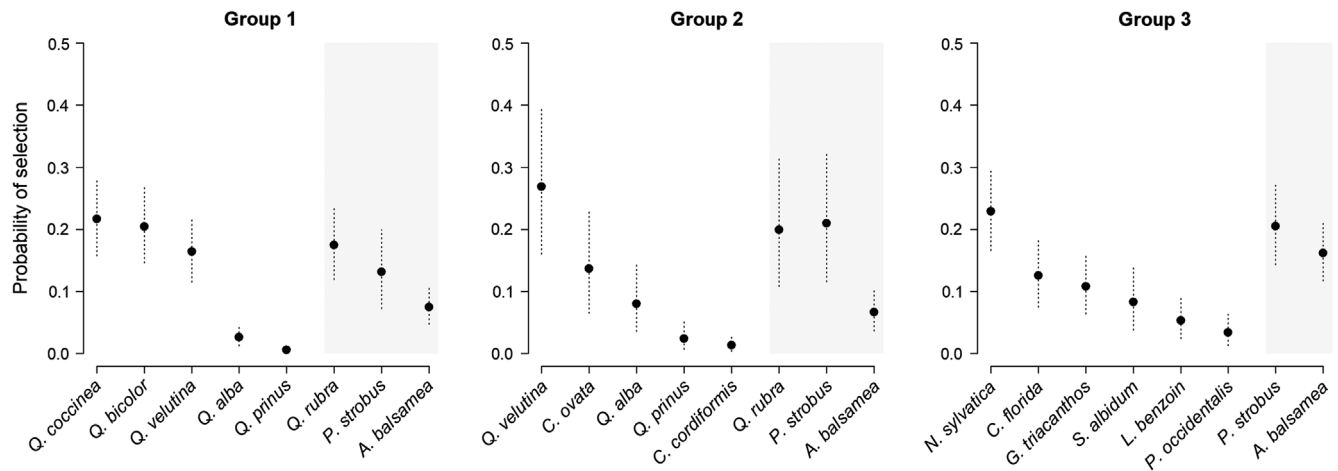


Figure 2. Probability of selection for each seed in the seed choice experiments (ranked from highest to lowest). The shaded area encompasses probabilities for the reference familiar seeds (*Pinus strobus*, *Abies balsamea* and *Quercus rubra* for group 1 and 2 only). The probability of selection was calculated taking into account the availability of each of the other seeds in the experiments. The values shown in the figure correspond to the probability of choice when each of the other seeds is 100% available. Group 1 = acorns, group 2 = acorns and hickory nuts, group 3 = medium sized seeds.

seeds than consuming them immediately ( $p < 0.05$ , reference category: American red squirrels).

### Seed fate experiments

The analyses conducted on tagged seeds showed that removed seeds had an equal probability of being predated or cached ( $p > 0.05$  for all seed species).

### Seed fate

#### Dispersal distance (*Quercus* and *Carya* only)

By fitting mixed-effects models on the dispersal distance of each seed (response variable), we found that the dispersal distance was greater for larger seeds and seeds with harder shells (top-ranked models are shown in Table 3; model predictions are shown in Fig. 4). The third-ranked model (within two delta AICc) included percentage lipids (positive relationship: larger dispersal distance for seeds with a higher

percentage of lipids), but we note that standard errors for parameter estimates were relatively large in this case.

#### Caching site

We found a higher proportion of seeds deposited on the forest floor (64% of the seeds,  $\chi^2 = 12.7$ ,  $df = 1$ ,  $p < 0.01$ ; comparison between forest floor versus buried and on trees), followed by buried seeds (34%  $\chi^2 = 45.06$ ,  $df = 1$ ,  $p < 0.01$ ; comparison between buried versus retrieved on trees) and a small proportion (2%) on trees.

#### Seedling emergence

Through our seed emergence experiments we found that seedling emergence proportions varied markedly among species, ranging from 0 to 85% (Supplementary material Appendix 1 Table A1). The mixed-effects binomial regression analysis supported a positive relationship between seedling emergence and seed mass ( $z$ -value = 2.2,  $p = 0.03$ ). The simple

Table 3. Traits affecting seed selection, seed fate and dispersal distance. Results for mixed-effects models with the following response variables: relative preference (i.e. difference with *A. balsamea*), consumption versus removal of a seed from the cage (binary response variable), dispersal distance. Model ranking according to  $\Delta AICc$  (delta Akaike information criterion); only models  $< 2 \Delta AICc$  are shown.

Model	$\Delta AICc$	Cumulative Akaike weights	$R^{2*}$
Relative preference			
Shell hardness	0	0.296	0.65
Seed mass (nat. log)	0.651	0.509	0.41
Percent carbohydrates	1.162	0.675	0.40
Consumption versus removal (seed choice experiments)			
Year	0	0.980	0.89
Dispersal distance			
Shell hardness + Seed mass (nat. log)	0.000	0.272	0.55
Shell hardness	0.457	0.489	0.54
Shell hardness + Seed mass (nat. log) + Percent	1.213	0.638	0.56
Percent lipids	1.874	0.744	0.55

\* All provided values are conditional  $R^2$  for the full model (including fixed and random effects).



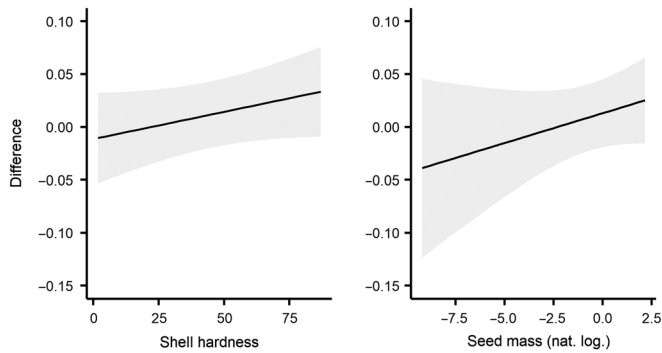


Figure 3. Model averaged predicted relationship (and 95% CI) between two seed traits (shell hardness – type D Shore scale – and seed mass) and the difference in the probability of selection of a given seed relative to the probability of selection of the reference balsam fir (*A. balsamea*). Positive values refer to higher preference compared to the balsam fir whereas negative values refer to lower preference compared to balsam fir.

correlation between proportion of seedlings emerged and seed mass was  $\rho = 0.5$  ( $p < 0.05$ ).

## Discussion

By exposing a naïve small mammal community to novel seeds predicted to expand in the northeastern United States in the near future, we demonstrated seed selection patterns that could impact future forest community composition. We found that novel seeds were not ignored, rather, the probability of selection of a novel seed varied among species and was, at times, higher than the selection probability of familiar seeds (Fig. 2). Our results show that seed traits rather than novelty/familiarity guide small mammals seed selection, specifically we found that shell hardness and seed mass both increase the probability of a seed being selected (Fig. 3).

We found that most seeds were initially removed rather than consumed; nevertheless, we found evidence that once removed a seed had an equal probability of being consumed or being cached, at least within the first days. In the case of acorns and hickory nuts, we also found that larger seeds and

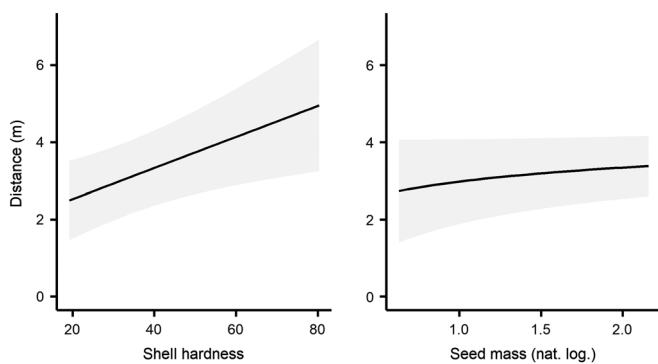


Figure 4. Model averaged predicted dispersal distance of seeds as a function of shell hardness (type D Shore scale) and seed mass.

seeds with harder shells were cached at a further distance (up to 30 m in our study system) (Fig. 4). Furthermore, we found 33% of seeds cached in optimal sites for germination such as buried in organic soil and leaf litter or near coarse woody debris (Smith et al. 1997). Finally, we found evidence that the role of small mammals may be modified by the higher emergence rates found for larger seeds (i.e. reinforced if a seed is dispersed or counterbalanced if a seed is predated).

Our findings are critical because most modelling efforts, and consequently management recommendations, tend to overlook the critical role played in range expansion by seed predators and dispersers such as small mammals. While more studies are needed to further quantify the role played by rodents, our results suggest that some generalizations are possible. In particular our results show that traits such as size and shell hardness may serve as a starting point for modelers and managers evaluating plant range expansion.

## Interactions between small mammals and novel seeds

By measuring the availability of seeds at each point in time we were able to infer resource selection rather than use. This distinction is important because, while it is known that rodents will consume ‘novel’ foods such as sunflower seeds and peanut butter, which are typically used as bait in field research, establishing whether novel seeds would be selected over familiar seeds in the field could not be assumed without empirical evidence. Our findings on seed selection are in line with previous studies conducted in areas of sympatry between these small mammal species and the target seeds of this investigation (Briggs and Smith 1989, Ivan and Swihart 2000). This may suggest that, where detailed field experiments such as ours are not feasible, existing empirical knowledge could potentially be used to assess how seed predators and dispersers influence plant range shifts. We note, however, that extensive gaps in the literature still exist, and we reiterate that small mammal community structure (i.e. the abundance/dominance relationships among species) may vary with latitude and longitude such that the cumulative impact on seeds may be substantially different between areas of sympatry and areas of expansion. Indeed many studies have also shown a link between per capita availability of seeds and dispersal consequences (Xiao et al. 2013). Our findings underscore the need for basic natural history studies and the unforeseen implications of these dynamics on the challenges that ecosystems face today, such as global climate change.

Our results suggest that rodents possess an innate ability to detect seed trait cues that will guide their seed selection. Very few previous studies have focused on this topic. Muñoz and Bonal (2008) found that learning played a critical role in decision making in *Mus spretus*, whereas Steele et al. (2006) found that grey squirrels (*S. carolinensis*) possess innate abilities that guide their choice and suggested that such abilities may have evolved as an adaptation to oaks, a key staple food for this species. The main predator–disperser in our system (*T. hudsonicus*) is specialized on conifer seeds rather than oaks

(Steele and Koprowski 2001) making it unlikely that this species may have evolved innate abilities for dealing with oak or hickory seeds (but see Goheen et al. 2004 for an example of morphological adaptations). Indeed, Weigl and Hanson (1980) found that naïve American red squirrels improved their exploitation of hickory seeds only following a six-week experiential learning period. Our results suggest that naïve squirrels have a very general, possibly innate, portfolio of skills that guides their seed selection. From an evolutionary perspective, developing a rather general seed-selection portfolio would allow a species to perform well in a variety of environments (e.g. such forest succession). We cannot exclude the possibility that our target species went through a very quick learning phase during the first hours of interaction with our cafeteria arrays; however, we emphasize that from an ecological and conservation standpoint, the implications of our findings remain unchanged.

### Seed traits override novelty

The observed preference for larger seeds (Fig. 3) corroborates previous research (Jansen et al. 2004, Vander Wall 2010, Lichti et al. 2017). Larger seeds provide more biomass and are thus a more profitable item (but see Gong et al., 2015). We acknowledge that our suite of ‘large seeds’ was mainly composed of acorns and hickory nuts; nevertheless, these are de facto the regional species most likely to expand in response to climate change (Prasad et al. 2007). Therefore from a heuristic perspective, these species represent the most appropriate sample for our study. The relationship between rodent seed selection and seed hardness (Fig. 3) is complex because on one hand seed hardness increases handling time (consequently lowers short-term profitability) (Gong et al. 2015), yet on the other hand harder seeds are often selected for caching as their perishability is lower (Vander Wall 1990, 2010).

Our results on the immediate removal of a seed from the experimental cage (Table 3) were expected because rodents prefer to interact with seeds in a safe environment (Lichti et al. 2017). Once the seeds are removed, the probability of being consumed or cached elsewhere are equal. Making extrapolations between these proportions and the number of seeds that will be consumed under completely natural circumstances is unwarranted. Nevertheless, our findings provide evidence that the proportion cached is not negligible. This supports the assumption that small mammals facilitate dispersal of a significant number of seeds. We emphasize that while the red squirrel is considered mostly a larder–hoarder and consequently a seed predator rather than disperser (at least for conifer seeds (Steele et al. 2005), but see Goheen and Swihart (2003)), in our sample the majority of seeds were scatter-hoarded, which is in line with findings of Dempsey and Keppie (1993) from nearby New Brunswick. We note, however, that we found only a small number of tagged seeds in trees, which are a preferred caching site for squirrels (Goheen and Swihart 2003). Future studies should focus on improving the detectability of seeds cached on trees

(e.g. by using radio-transmitters), as these are unlikely to germinate successfully.

Our caching results suggest that a notable proportion of seeds are cached in an optimal place for regeneration such as on or near coarse woody debris, or under leaf litter or surface soils (Smith et al. 1997). Small mammals’ facilitation of germination has been addressed before (Jansen et al. 2004), but future research is needed to establish if and how facilitation patterns differ with range-shifting plants (i.e. plants that are not within their optimal conditions). Our findings suggest that the overall role played by the small mammal community in our system is to both predate and disperse novel seeds, which is in line with existing knowledge in areas of sympatry (Vander Wall 1990, Lichti et al. 2017). In particular we emphasize that site and time specific factors, such per capita availability of seeds, may determine a prevalence of predation versus dispersal or vice versa (i.e. variation in the positioning on the predation – mutualistic relationship) which implies that at a given site the balance may be towards dispersal one year and towards predation another year. We identify these as key research areas for future studies.

### Seed size affects plant emergence

Our emergence experiments emphasize the potential for the oaks and hickories, in particular, to be assisted in their climate-driven range expansion by small mammal seed dispersers. These species had higher emergence success and, notably, were preferentially selected by small mammals and were dispersed more often and at further distances.

The seedling emergence data are only from a single season, making this study limited in assessing these early life stages for species planted beyond their range limits. Results varied widely among species and this may relate to weather, seedbed conditions and other uncontrolled factors. We also note that smaller seeds may be produced in larger numbers and this may counter-balance the lower emergence. Regardless, the findings are in line with other seedling establishment experiments indicating that this phase is a key bottleneck influencing forest composition and range expansion (Monahan and Fisichelli 2014). Where applicable (i.e. outside conservation areas or where the seed tagging allows it) future studies should consider estimating dispersal rates tracking seeds for longer time periods (i.e. months), allowing for the calculation of indices such as the seed dispersal effectiveness (Schupp et al. 2010) and it would also be important to place each species on a predator–mutualist continuum (Zwolak and Crone 2012). Further, we recommend that future seed dispersal studies focusing on ‘novel’ seeds also consider the critical role played by rodent population density (Lichti et al. 2017), the availability of seeds (Xiao et al. 2013) as well as the important role of individual-level factors such as personality (Brehm et al. 2019).

Seed dispersal distances found here corroborate those from previous studies. These distances, combined with fact that rodent densities can exceed 100 per hectare

(Krebs 2013), highlight the potential impact rodents have on seed dispersal and predation in the context of plant range expansions. Other factors such as landscape permeability and forest edges (Levey et al. 2005, Mazzamuto et al. 2018) will also play a key role as they may affect rodent abundance and behavior and should be considered priorities for future research.

### Small mammals as regulators of plant range-expansion

Taken together, our empirical findings suggest that small mammals may play an important role in facilitating climate-induced range shifts in plants. During the initial phase of expansion, the first plant arrivals may be largely outnumbered by seed predators and dispersers, therefore the role played by small mammals may be disproportionately large. We note that the range of key rodent seed predators and dispersers in the United States (*Sciurus*, *Tamiasciurus*, *Peromyscus*, *Myodes*) is large enough to encompass numerous plant range limits, such as the ones described in this paper (Fig. 1). It follows that many of the novel interactions that we have depicted will occur at the population rather than the species level: the first plant dispersers will experience naïve rodent populations rather than new rodent species (see also Supplementary material Appendix 1). As previously mentioned, this may be useful from a conservation perspective as it suggests that empirical data from areas of sympatry could be valuable for predictive purposes. We note that the pattern highlighted here is mirrored in Europe, where the main seed predators (*Sciurus*, *Apodemus* and *Myodes*) have geographical ranges large enough to encompass numerous plant range limits (Mitchell-Jones et al. 1999).

In this study we have focused on rodents but we acknowledge that other animals, such as birds, are also important dispersers and may disperse seeds over longer distances. Dispersal complementarity is widespread and consists of dispersal provided by multiple species where some species provide dispersal at a local scale, whereas others provide long distance dispersal (Spiegel and Nathan 2007, Schupp et al. 2010). As an example, within our system rodents are likely to move large numbers of seeds over small distances, whereas jays are more likely to move seeds at longer distances (Chambers et al. 1999). We point out that while the literature emphasizes long-distance dispersal (Nathan et al. 2008), from a seed dispersal effectiveness perspective, both may be equally important or, in some instances, local dispersal may be more important (Schupp et al. 2010).

Incorporating the influence of seed predators and dispersers in range-expansion models will be challenging, but we believe it is essential to management and conservation. Not only will small mammal densities vary in space and time (Krebs 2013) (meaning the effects on seeds may vary substantially across geographic areas and across years), but successful expansion will also depend on additional variables such as

recent disturbance, dispersal barriers, browsing pressure and other seed predators and dispersers such as birds (Dennis et al. 2007). Future studies should focus on obtaining additional information to help parameterize increasingly realistic models, thereby enabling modelers and managers alike to better predict climate-induced species range expansions.

### Speculations

In a recent work Brehm et al. (2019) found that an individual's personality affects its choice of seeds, as well as how distant and where seeds are cached. Based on these previous findings we speculate that an individual's personality will affect the interaction with novel seeds; in particular, following Brehm et al. (2019) we predict that bolder and less anxious individuals will be more likely to interact with novel seeds. Further, Brehm et al. (2019) found that land-use change shifts the distribution of personalities within a population, by increasing the proportion of bold, active and anxious individuals and in-turn affecting the potential survival and dispersal of seeds. We thus speculate that small mammal controls on the climate-driven range shift of woody plant species may be also mediated by land-use change effects on the distribution of personalities within a population.

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