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Small mammal granivory as a biotic filter for tree establishment beyond elevation range boundaries

Jordon Tourville[1,2] · Martin Dovciak[1]

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Abstract
Trees often experience migration lags in their response to rapidly changing climate. Preferential granivory by nocturnal small mammals has the potential to create lags by reducing germination success beyond range edges. To determine how granivory may limit establishment of trees beyond their range margins, we conducted a seed choice experiment which offered seeds of five regionally dominant tree species to small mammals within distinct forest communities across a 400 m elevational gradient on four mountains in the northeastern United States. Multinomial logistic mixed-effects models were used to (a) quantify seed preference of each species across the elevational gradient and (b) assess relationships between seed preference and abiotic variables. A separate seed dispersal experiment was used to compare the probability of seed consumption versus seed caching. The low elevation temperate tree species *Fagus grandifolia* and *Acer saccharum* had an equally high probability of granivory within and beyond their range margins (~40% and ~20%, respectively). Generally, seed preference was positively correlated with seed mass and nutrient content regardless of elevation. Our seed dispersal experiment revealed that seeds were 3 × more likely to be consumed than cached, suggesting that small mammals can potentially decrease germination success. Overall, temperate tree species with either high seed mass or nutritional value may experience substantial granivory beyond their range margin, partially explaining the observed lag between tree dispersal and climate change. Thus, granivory is vital to consider when modeling future tree species distributions under various climate change scenarios.

Keywords Granivory · Climate change · Range expansion · Small mammals · Northern hardwoods · Spruce-fir

Introduction

Many temperate deciduous woody species are expected to migrate to higher latitudes and elevations as a result of climate warming (Boisvert-Marsh et al. 2014; Harsch et al. 2009; Lenoir and Svenning 2015). Much effort has been devoted to modelling future tree species distributions in order to inform pragmatic forest management and conservation in the face of climate change (Iverson et al. 2008, 2019; Prasad et al. 2020; Wisz et al. 2013). Unfortunately, biotic interactions are usually absent from these models (Alexander et al. 2018; Araújo and Luoto 2007; HilleRisLambers et al. 2013; Wisz et al. 2013). Yet, biotic interactions can shape the realized niche space of individual tree species, greatly influencing their ability to establish in novel environments, and potentially altering their future distributions. While data on biotic interactions are more labor intensive to collect, often harder to measure, and in many cases context-dependent at small spatial scales, this information is still critical to consider (Klanderud et al. 2015).

Several studies have provided evidence to suggest that tree species are not migrating poleward or upslope at a rate predicted to keep pace with climate warming (Foster and D'Amato 2015; Sittaro et al. 2017; Wason and Dovciak 2017; Zhu et al. 2012); and this seems to be the case particularly for deciduous temperate tree species (at least in northeastern U.S.; Tourville et al. 2022). Context-specific biotic interactions may slow or inhibit tree establishment via a variety of mechanisms, and this can be further complicated by global change drivers (Alexander et al. 2018; Jones and

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✉ Jordon Tourville
jtourville@outdoors.org

[1] Department of Environmental Biology, State University of New York College of Environmental Science and Forestry (SUNY-ESF), 1 Forestry Drive, Syracuse, NY 13210, USA

[2] Research Department, Appalachian Mountain Club, P.O. Box 298, Gorham, New Hampshire 03818, USA

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Gilbert 2016; Liang et al. 2018; Lynn et al. 2019; Neuschulz et al. 2018; Savage and Vellend 2015). Herbivore interactions with plants have the potential to greatly influence plant establishment success (HilleRisLambers et al. 2013). In particular, several studies have suggested that mammalian herbivory in general can influence forest response to climate warming by reducing the competitive dominance of deciduous trees and shrubs expanding into areas beyond their range margins, leading to a so-called "cooling" effect (Fisichelli et al. 2012; Post and Pedersen 2008). However, granivory, particularly involving small mammals, has received far less attention as agents driving this "cooling" effect, especially when considering work done with other mammals, insects, or birds (Godó et al. 2022; Mortelliti et al. 2019). Increased seed predation outside of species range limits could act as a form of an Allee effect (cf. Alexander et al. 2018; Brown and Vellend 2014; Courchamp et al. 2008) and limit the migration of a tree species resulting in a migration lag that conforms to the empirical observations taken from many studies across both latitudinal and elevational gradients (Alexander et al. 2018; Brown and Vellend 2014; Sittaro et al. 2017; Zhu et al. 2012). In contrast, seed predation declining beyond species range limits (cf., Janzen-Connell hypothesis, negative density-dependence, enemy release hypothesis; Hillyer and Silman 2010; Van der Putten et al. 2010; Wang 2020) could facilitate species migrations (and counter to some degree species migration lags).

A growing number of authors have discussed the role of small mammal granivory affecting tree species establishment across the temperate-boreal forest ecotone (TBE) in northeastern North America (Brown and Vellend 2014; Evans and Brown 2017; Fisichelli et al. 2012; Mortelliti et al. 2019). Research suggests that the encroachment of dominant temperate deciduous canopy tree genera such as *Acer*, *Fagus*, *Quercus*, and *Betula* into boreal forests at high latitudes and elevations can be inhibited by preferential mammalian granivory (Boone and Mortelliti 2019; Brown and Vellend 2014; Evans and Brown 2017; Olofsson et al. 2009; Urli et al. 2016). Brown and Vellend (2014) documented increased granivory of sugar maple at high elevations beyond its range margin, caused mainly by small mammals (rodents). Cafeteria-style studies of small mammal granivory have revealed preference for southern species expected to migrate poleward as climate warming continues; modulated somewhat by seed size, seed nutrient status, and level of familiarity of seed predators with seed species (Boone and Mortelliti 2019; Mortelliti et al. 2019). The seeds of several temperate deciduous tree species in the region are larger, more palatable, and have a higher nutrient content than common boreal conifer species present, therefore, species with these seed traits should be highly prized by mammalian granivores (Evans and Brown 2017; Johnson and Zettlemoyer 2022; Myers-Smith et al. 2011; Sundaram et al. 2015, 2018). However, both a seed transplant experiment (Hillyer and Silman 2010) and a common garden experiment (Rokaya et al. 2016) revealed increased seed survival and decreased foliar damage of low-elevation plant species at higher elevations, dependent on plant species identity and the identity of the dominant seed predator, possibly suggesting an enemy escape mechanism. Thus, the role of granivory on the dispersal, germination, and recruitment potential of seeds in northeastern forests seems highly dependent on the granivores present, seed species, seed size, and seed nutritional value (Johnson and Zettlemoyer 2022).

Seed preference and seed survival may also be complicated by environmental and behavioral factors. Boone and Mortelliti (2019) found that choice of seed, depending on the mammal species making the choice, was influenced by abiotic variables such as nighttime illumination (for nocturnal species; dictated by moon phase), rain, and temperature. These factors likely act to alter the perception of predation risk of small mammals (mainly nocturnal foragers) which can create temporal patterns in seed selection preferences (Orrock et al. 2004; Perea et al. 2011). Additionally, vegetation structure can also influence the spatial patterns of granivore seed selection, with different field conditions (open vs. closed canopy, high vs. low shrub cover, etc.) either increasing or decreasing granivore activity (Boone et al. 2022; Chen et al. 2022; Dammhahn et al. 2022). Further, while seed consumption would inhibit tree range expansion and support a "cooling" effect, seed hoarding and caching behavior could help facilitate expansion by enhancing seed dispersal into favorable germination conditions (Vander Wall 2010; Zwolak 2018; Zwolak and Crone 2012). Thus, it is critical to determine the ultimate fate of seeds that are selected by resident small mammals. Since some highly nutritious temperate deciduous seeds would be found at low densities beyond their range margins it seems likely that most seed-granivore interactions would result in immediate consumption rather than caching (Brown and Vellend 2014; Rivest and Vellend 2018; Urli et al. 2016; Boone and Mortelliti 2019).

The purpose of this study is to assess the role of small mammalian granivores in limiting the expansion of low elevation temperate deciduous trees into high elevation spruce-fir boreal forests across the TBE in northern New England (testing the 'cooling' effect). In order to address this objective, we conducted two separate field-based experiments. The first experiment was used to quantify levels of seed removal, seed species preference, and relationships between seed preference and abiotic variables. The second experiment was designed to determine the most likely fate of selected seeds: consumption vs. caching. Here, we assume that increased seed caching behavior will ameliorate the negative impact of seed predation on seed germination success rates. We hypothesized that seed selection of northern hardwood tree species would be much greater at higher elevations (beyond their range margins) than at lower elevations (in their current range) (Hypothesis 1, H1), and further, that seeds with greater mass and nutrient content (protein and lipids) would have a greater chance of selection than smaller, less nutritious seeds (Hypothesis 2, H2). We also hypothesized that nighttime illumination level, rain, temperature, and vegetation type would significantly influence seed preference (seed choice) probabilities (Hypothesis 3, H3). Lastly, the type of seed-granivore interaction, either facilitative or inhibitory, would depend on the relative probability of a seed being consumed vs. cached by the resident small mammal community, and we hypothesized that offered seeds would more likely be consumed than cached (Hypothesis 4, H4).

Methods

Study area

Our study was conducted across elevation gradients on four mountains in the Green Mountains of Vermont (Fig. 1): Mt. Abraham, Mt. Mansfield, Jay Peak, and Killington Peak. These mountains maintain clear transitions between temperate deciduous northern hardwood forest communities (*Acer saccharum* Marshall*,* sugar maple; *Betula alleghaniensis* Briton*,* yellow birch; *Fagus grandifoila* Ehrh., American beech) which dominate the lower slopes on mountains across the region, and coniferous spruce-fir forests (*Picea rubens* Sarg., red spruce; *Abies balsamea* (L.) Mill., balsam fir) which dominate the upper slopes (Lee et al. 2005; Reiners and Lang 1979; Siccama 1974). A distinct ecotone around 800 m above sea level (asl) separates these forest community types, with some scattered trees of the dominant species of each forest type found in the adjacent forest types. It is important to note that American beech and sugar maple are the most dominant tree species in low-elevation hardwood forests, and that red spruce individuals can also be found at low elevations.

The region is characterized by short hot and humid summers and long harsh winters. Across the four mountains, mean daily minimum temperatures range from −1.5 to −0.6 °C, mean daily maximum temperatures from 8.3 to 10.1 °C, and mean annual total precipitation from 130 to

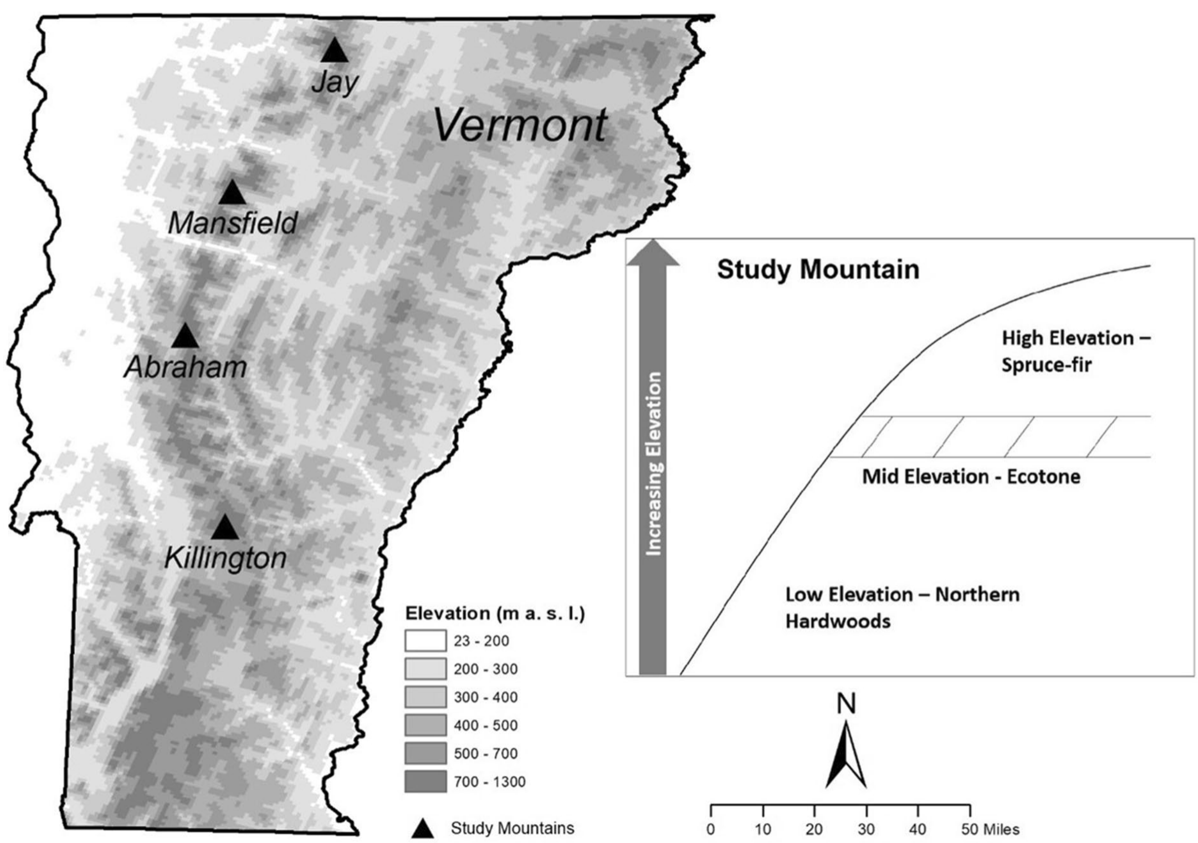

Fig. 1 Map displaying the location of the four study mountains within the Green Mountains of Vermont. Darker areas indicate areas of high elevation (> 700 m). The inset depicts a simplified representation of how forest communities change across the elevation gradient. Mountains include Mt. Abraham (UTM 665126E 4887319N Zone 18), Mt. Mansfield (UTM 673624E 4934600N Zone 18), Jay Peak (UTM 695270E 4977503N Zone 18), and Killington Peak (UTM 675924E 4830280N Zone 18)

149 cm (PRISM Climate Group, Oregon State University, https://prism.oregonstate.edu). As elevation increases from 550 to 1160 m asl, mean annual temperature decreases from 5.2 to 1.3 °C, frost free days decrease from ~ 150 to ~ 80 days per year, maximum snow depth increases from 60 to 120 cm, and growing season precipitation increases from 40 to 60 cm (Siccama 1974). The region has experienced warming of 0.25 °C per decade since 1970, with greater warming occurring in winter than in summer (Cooter and Leduc 1995; Hayhoe et al. 2008; Kunkel et al. 2013). Annual precipitation has generally increased (Hayhoe et al. 2008; Kunkel et al. 2013) with less precipitation during the summer and less precipitation falling as snow in winter (Huntington and Hodgkin 2003). The most abundant small mammal species in the region include deer mice (*Peromyscus maniculatus*), southern red-backed voles (*Myodes gapperi*), northern short-tailed shrews (*Blarina brevicauda*), North American red squirrels (*Tamiasciurus hudsonicus*), *Sorex* spp., woodland jumping mice (*Napaeozapus insignis*), northern flying squirrels (*Glaucomys sabrinus*), and eastern chipmunks (*Tamias striatus*) (Miller and Getz 1977). Deer mice, southern red-backed voles, northern short-tailed shrews, woodland jumping mice, northern flying squirrels, and eastern chipmunks are known to inhabit both northern hardwood and spruce-fir forests found across our elevation gradient while red squirrels are much more common in high elevation spruce-fir forests (DeGraaf and Yamasaki 2001; Miller and Getz 1977).

Study design

Three sites were selected on each of the four mountains (12 sites total) encompassing the full diversity of forest communities across the elevation gradient. The low elevation site (northern hardwoods) was located at 600 m asl; the mid elevation site (ecotone) was located at 800 m asl, and the high elevation site (spruce-fir) was located at 1000 m asl. Within each site, eight locations were staked out 50-m apart along elevation contours. Five randomly placed stations served as locations for seed trays as part of the seed selection experiment (see below) and three randomly chosen locations were used for the seed dispersal experiment. Microhabitat variables were measured at the sites of the seed selection experiment on 1 × 1 m plots (all 5 per site) in another study (Tourville et al. 2022). These include slope, aspect, microtopography (flat, hollow, mounded, or transitional), canopy openness (as measured by densiometer), and the percent cover of mineral soil, exposed rock, coarse woody debris (CWD), and vegetation type (partitioned between tree seedlings, herbaceous forbs, shrubs, graminoids, ferns, clubmosses, and bryophytes).

Seed selection experiment

Seeds of five regionally dominant tree species were offered in a cafeteria-style experiment in the fall of 2020 (mid-September through mid-October), coinciding with the timing of natural seed release and dispersal of our focal tree species (Burns and Honkala 1990). The focal tree species included American beech (*Fagus grandifoila*), sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), balsam fir (*Abies balsamea*), and red spruce (*Picea* rubens). All seeds were purchased from either Shefield's Seed Company (Locke, NY) or F.W. Schumacher Seed Company (Sandwich, MA). Seed species were offered in equal amounts by mass (3 g per station) to standardize across species with various seed sizes (Boone and Mortelliti 2019). Seeds were offered to mammals as they would naturally be found post-dispersal on the forest floor (conifer seeds removed from cones and sugar maple wings attached).

At each seed selection station, five petri dishes (6 cm diameter) were afixed to one wooden plank with Velcro strips (see Fig. 2). The planks were fixed to the ground with two metal lawn stakes to ensure stability. We opted not to enclose each station with a wire cage. While a cage would fully ensure exclusion of any non-target species (i.e., birds, large mammals), it also has the potential to discourage visitation by target species (Mortelliti, *personal communication*). We believed non-target visitation to seed stations would be low given the dense understory of the sites. In each petri dish seeds of one species were placed. Species were randomly assigned to a dish at each site. All stations were checked daily for damage, cleaned of debris, and were removed after four nights. Seeds were not replaced after each daily check. At noon on the last day of deployment, any remaining seeds were collected in order to compare the final mass of seeds remaining for each species. Stations were then moved and redeployed on each of the remaining mountains for a total of 60 deployed stations at 12 distinct sites (elevations) across 16 total days.

Small mammal seed choice was determined using infrared game cameras (see SI for examples of videos). At each station, a Stealth Cam G45NG Pro camera was attached to a tree within 1 m of the dishes. The camera was angled down between 45 and 60 degrees to provide a full view of the station. All cameras were setup to record 30-s videos at 1080 HP, and with a 5-s trigger delay between videos when triggered using a near-field setting. In addition to seed choice and mammal species identification and behavior, the cameras were also used to record temperature, time, and the presence of rain at the time of each seed selection event. Sample videos were taken in the field prior to full deployment to ensure camera alignment with seed stations.

Fig. 2 Layout of each seed selection station. Seed species are labeled in the left photo (*ACSA* sugar maple; *BEAL* yellow birch; *PIRU* red spruce; *ABBA* balsam fir; *FAGR* American beech), while the right photo shows how cameras were placed near seed stations

Seed dispersal experiment

In each of the 12 sites, 3 seed dispersal stations were established to track dispersal distances of seeds and their ultimate fate (consumption vs. caching). Only American beech seeds (beechnuts) were used in this experiment as retrieval tags could not be fixed to the smaller seed species. To track beechnut dispersal, a length (1 inch) of yellow yarn was attached to the side of each seed using solvent-free glue, as detailed by Kempter et al. (2018). At each seed dispersal station, 30 beechnuts were placed on a small wooden platform secured to the ground with lawn stakes. The seeds were left uncaged as in the seed selection experiment. An infrared camera was afixed to a nearby tree within 1 m of the station to allow for small mammal identification and quantification of behaviors at the time of seed removal. After three nights a 2-h, grided systematic search up to 30 m away from the station was conducted for the tagged beechnuts. When one was found, we recorded distance away from the station, whether it was consumed or not, and the substrate in which the seed was found (either found on the surface of the forest floor, buried under the litter mat, or found on a tree). Across all sites, mean recovery rate for tagged beechnuts was 76%.

Data collection and processing

All 30-s field videos were processed to determine seed preferences by the resident small mammal community. Seed choice events were defined as the discrete times a small mammal handled a seed in any way. For each observed seed choice event we recorded time of day, the small mammal species, the seed species chosen, the number of seeds consumed per event, seed availability (the number of seeds remaining visible in the video) for all seed species, temperature, whether it was raining or not, illumination level, and handling time for the seed species during the event. The high quality of the video taken allowed us to count the number of seeds that were taken or consumed during each event. Running counts of remaining seed number at each station allowed for easy calculation of seed availability for each seed species. This number was divided by the total number of starting seeds to provide seed availability as a proportion. Time, rain, and temperature were taken directly from the video and camera metadata. As most seed predation events occurred during the night, illumination was characterized by the moon phase at the time of the event (new, crescent, quarter, gibbous, full, and a category for daytime light when events occurred during daylight hours). Local weather reports and the time and day of the seed predation event were used to determine the moon phase during each event. Seed handling time was measured with a stopwatch and was defined as the time between when a seed was first picked up and when it was fully consumed or dropped. Events where the end point could not be determined because the video ended before it occurred, or the mammal carried the seed outside the video frame were not used for handling time calculations.

Data analysis

Seed preference was determined by fitting multinomial logistic mixed effects models to seed choice data within a Bayesian framework. The seed species selected for each predation event was used as a categorical response variable. Site (seed station) was included as a random effect nested within mountain to account for mountain specific differences in seed selection as well as the potential dependence between the choices made at the same site by the same individual animal visiting multiple stations. We used seed choice data from all observed small mammal species as we were interested in the seed consumption activity of the small mammal community as a whole, and because of the high proportion of videos involving white footed mice. Seed availability for each seed species (measured as a proportion from 100% availability) was included as a fixed effect in all models. Temperature, time, illumination, rain, and microhabitat variables (microtopography and cover totals of various plant groups) were sequentially added to individual models as fixed effects (see Supplemental Table S1 for description of all fixed effects). Multicollinearity between continuous variables was assessed by examining variance inflation factors (VIF) and determined to be low in all models (<2.5). All continuous variables were z-score transformed and centered, and all circular variables (i.e., time and aspect) were linearized. Specifically, time was transformed to a proportion of time elapsed since the beginning of the day (from midnight, see Koster and McElreath 2017), and aspect was transformed via the following equation from McCune and Keon (2002):

$$180 - Aspect - 180 \tag{1}$$

Models were fit using the R packages 'rethinking' and 'Rstan' (version 4.0.3) (R Core Team, 2020) following the procedure laid out by Koster and McElreath (2017). Following this procedure, all fixed effects were assigned uninformative priors. Our models used 1000 warm-up iterations, and three chains each containing 2000 iterations. Traceplots helped assess model convergence and ensure suitable mixing. Number of effective samples and Rhat values (Gelman-Rubin convergence diagnostic) served as a check of model performance.

Model comparison was facilitated using the Widely Applicable Information Criterion (WAIC) (Hooten and Hobbs 2015). Strong model performance was linked to models within two ΔWAIC of the top model (see Boone and Mortelliti 2019). Seed selection was inferred based on the predicted values for selection probability with uncertainty visualized with 89 percentile credibility intervals (see McElreath, 2020 for discussion of 89 percentile credible intervals). Our top model was used to evaluate seed selection probability for each elevation (a proxy for forest type) to visualize differences in seed selection across the elevation gradient (testing H1). A two-way ANOVA and post-hoc Tukey's HSD test were used to detect differences in seed mass removed by species and elevation as a separate and independent test of H1 (see Supplemental Information).

Mean seed mass was calculated using ten seeds per species and nutritional information and seed traits for each species was recorded from available literature and from the Seed Information Database of Kew Gardens (Table 1) (Boone and Mortelliti 2019; Sundaram et al. 2015). Since only a small number of seed species were analyzed, we decided to use mean species seed traits in a qualitative way (not as model predictors) to form broad conclusions on their effects on the probability of selection (testing H2). Seed preference as a function of abiotic variables included as fixed effects in our top model was visualized in order to detect the direction and magnitude of their relationships (testing H3). Seed dispersal data for tagged beechnuts were analyzed by fitting a linear mixed-effects model with a binary logistic response variable (seed retrieved consumed versus seed retrieved intact) using site as a nested random effect within mountain and fit using the 'lme4' package in R (testing H4). Pairwise differences between all substrate types for cached seeds were explored and analyzed with a $\chi2$-test.

Results

Seed selection study

We collected and processed 1498 game camera videos from all study sites. Excluding videos triggered by wind or non-target animals we counted 1044 seed choice events involving seven target small mammal species: deer mice, red squirrels,

Table 1 Seed trait values for the five dominant canopy tree species examined in this study. Handling time (mean time each seed was processed by mammals), mean seed mass, and kcal/g were used to calculate kcal/seed and kcal/seed/sec

Seed species	handling time (sec)	Mean seed mass (g)	kcal/g	kcal/seed	kcal/seed/sec	Protein (%)	Carbohydrates (%)	Fat (%)	Moisture (%)
Balsam fir	2.64	0.00734	6.16	0.04521	0.01713	18.1	23	50.2	5.75
Sugar maple	5.34	0.05881	5.17	0.30405	0.05694	29.8	31.4	29.2	7.92
Yellow birch	4.23	0.00611	4.86	0.02969	0.00702	12.4	57.1	19	6.65
American beech	7.39	0.294	7.87	2.3138	0.31309	21.75	14.66	55.3	16.68
Red spruce	2.02	0.00302	5.83	0.01761	0.00872	27.4	18.8	44.2	4.71

Nutritional values of balsam fir and red spruce were taken from Boone and Mortelliti (2019). Values for American beech was taken from Sundaram et al. (2015), and values for sugar maple and yellow birch were derived from Seed Information Database of Kew Gardens

Table 2 Summary of seed choice events by small mammals and elevation

Mammal species	Species code	Number of seed choice events	% of total	NH	ECO	SF
North American Deermouse	PEMA	793	77.75	269	272	252
Red Squirrel	TAHU	83	8.14	0	50	33
Southern Red-backed Vole	MYGA	44	4.26	0	6	38
Eastern Chipmunk	TAST	43	4.22	30	13	0
Northern Flying Squirrel	GLSA	30	2.94	0	27	3
Woodland Jumping Mouse	NAIN	14	1.37	7	5	2
Northern Short-tailed Shrew	BLBR	13	1.27	0	1	12

A seed choice event was defined as anytime a target small mammal picked up a seed ($n = 1020$ events). Elevation is denoted by: *NH* northern hardwoods/low elevation; *ECO* ecotone/mid elevation; *SF* spruce-fir/high elevation

eastern chipmunks, southern red-backed voles, northern flying squirrels, woodland jumping mice, and northern short-tailed shrews (Table 2). The majority of seed selection events (77.75%) involved deer mice. While the number of seed choice events remained consistent for deer mice across the elevation gradient, the number of events for other small mammal species differed across elevation (Table 2). A small number ($n = 24$) of seed predation events from three non-target species, eastern cottontail (*Sylvilagus floridanus*), fisher (*Pekania pennanti*), and dark-eyed junco (*Junco hyemalis*), were removed from the dataset.

The probability of selection for American beech and red spruce seeds were both much higher than the other study seed species (~40% relative probability of selection, Fig. 3). While sugar maple was about half as likely to be selected than American beech and red spruce (~20% relative selection probability), it was twice as likely to be selected than balsam fir and yellow birch, both of which were very unlikely to be selected by the local small mammal community (<10% relative selection probability). Since there was no difference in seed selection probabilities between different elevations, and hence, different forest communities, selection probability for the hardwood species American beech and sugar maple, and the conifer species red spruce remained high across the elevation gradient, and beyond the upper range margin for both beech and sugar maple (Fig. 4, Supplemental Table S2). Seeds with the highest preference tended to have the highest mass and energy return in kcal/seed/second, with the exception of red spruce (Table 1). Within seed species there were no significant differences in the mass of seed removed across different elevations, however, significantly more American beech, red spruce, and sugar maple seed was removed than either balsam fir or yellow birch (Supplemental Figure S1; $p < 0.0001$).

The best multinomial model of seed preference as determined by WIAC included a small positive effect of illumination (with all seed species included), a mixed effect of seed availability (positive for American beech, red spruce, and sugar maple; negative for balsam fir and yellow birch), and a small effect of temperature on seed selection probabilities (see Supplemental Table 2 for parameter posterior means). The next best models included small effects of rain and site microtopography on selection probabilities (Table 3).

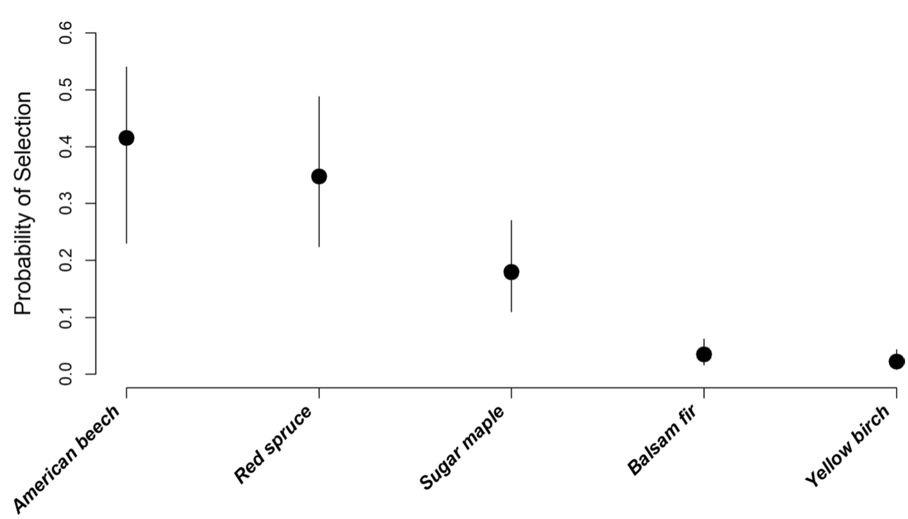

Fig. 3 Relative probability of selection by all small mammal species for each seed species. Solid lines represent 89% percentile credibility intervals

Fig. 4 Relative probability of selection by all small mammals of each dominant seed species at each of the three elevations (Northern Hardwoods = low elevation; Ecotone = mid elevation; Spruce-fir = high elevation) based on top model (see Table 3). Solid lines represent 89% percentile credibility intervals. Note that the y-axis scale is not the same for all species panels

Table 3 Model ranking for multinomial logistic regression models compared using ΔWAIC (delta Widely Applicable Information Criterion)

Model	Model code	WAIC	ΔWAIC	weight
Availability + illumination + temperature	SF1a	2619.01	0.00	0.58
Availability + illumination + temperature + rain	SF1	2620.09	1.08	0.34
Availability + illumination + temperature + rain + microtopography	SF2e	2624.72	5.70	0.03

Models < 2 ΔWAIC are considered the best models. We show the top three models. Availability = the availability of each seed species at the time of each seed selection event. Illumination = light levels by moon phase (1 = new moon; 2 = crescent; 3 = quarter; 4 = gibbous; 5 = Full; 6 = daylight). Temperature = temperature (˚C) at time of selection event. Rain = precipitation during selection event. Microtopography = microtopography at seed station (1 = flat; 2 = mounded; 3 = hollow; 4 = transitional)

Although the credibility intervals around these trends were quite large, increased illumination decreased selection probabilities for yellow birch and American beech, and increased selection probability of sugar maple (Supplemental Figure S2).

Seed dispersal study

Of the 821 (out of a total of 1,080) beechnuts that were recovered, 75% ($n = 616$) were consumed at the site they were offered (dispersal distance = 0 m). Deer mice and red squirrels were the most common granivores to visit the seed dispersal stations. The seeds had a greater chance of being consumed than being cached ($p = 0.001$). The frequency of seeds that were removed and dispersed decayed sharply with distance and no tagged seeds were recovered beyond 11 m (Fig. 5). Cached beechnuts were recovered in equivalent amounts between the forest floor (39.7%) and buried (35.3%) ($\chi 2 = 0.004$, df = 1, $p = 0.95$), between the forest floor and on a tree (25%) ($\chi 2 = 0.779$, df = 1, $p = 0.38$), and between buried and on a tree ($\chi 2 = 0.0971$, df = 1, $p = 0.76$).

Discussion

Even though there was no difference in seed selection patterns or mass of seed removed at different elevations, we found that seeds of the two most dominant low elevation deciduous tree species (beech and maple, but not the small-seeded yellow birch) were highly prized both within and

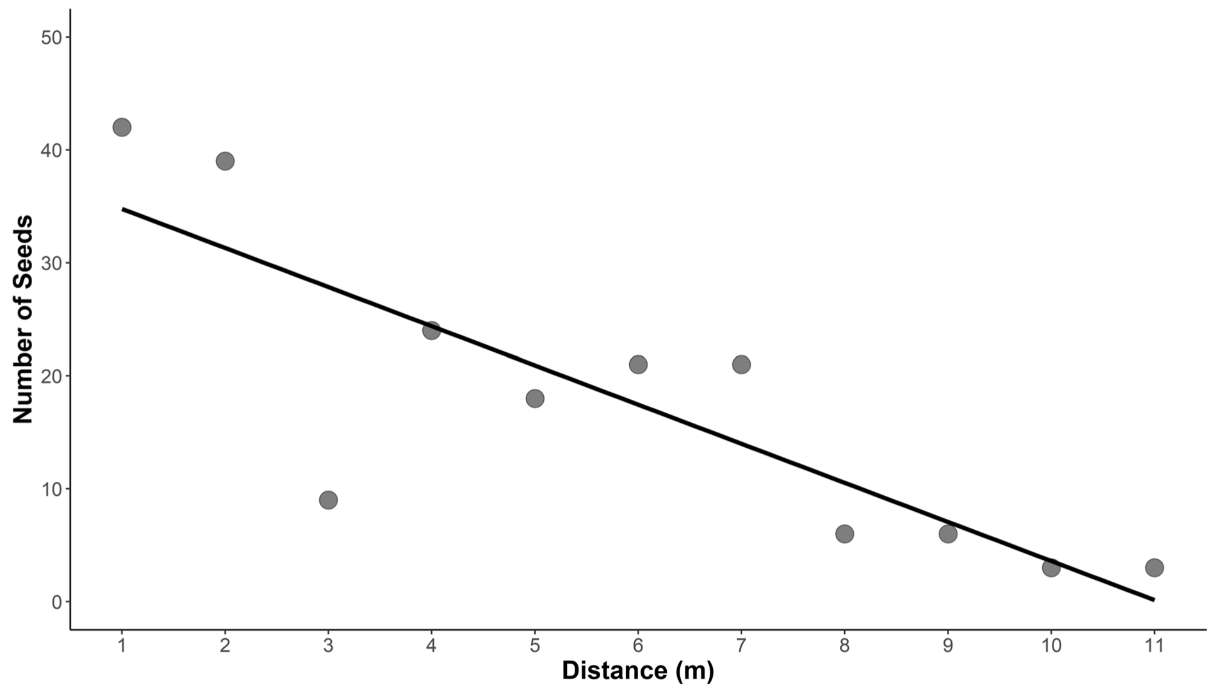

Fig. 5 Frequency of recovered intact beechnuts as a function of distance (m) from seed stations in the seed dispersal experiment. Points are binned within 1 m intervals. Beechnut number decreased monotonically with distance and no beechnuts were recovered farther than 11 m from the seed stations ($p=0.001$; $R^2=0.67$). There were no significant differences in caching substrate for dispersed beechnuts

beyond their range margins, despite these seeds being normally absent or only found in low abundance at high elevation sites (partially supporting H1). Thus, we cannot invoke either a potential Allee effect from increased seed predation across range boundaries or a reduced seed predation enemy-release mechanism in this study. While the number of seed selection events changed dramatically for most mammals across the gradient, it remained consistent for deer mice which comprised the majority of observed events (77.75%). If deer mouse seed preferences are driving the observed patterns of seed selection, this could explain the maintenance of selection probabilities at different elevations, particularly if mouse populations fluctuate with seed masting years which have been observed to be synchronous between beech and sugar maple (Cleavitt and Fahey 2017). The novelty of a seed does not seem to imply that it will be less preferred by native small mammal communities. A recent study by Mortelliti et al. (2019) offering both native and novel seeds to small mammals revealed that seed mass and other seed traits predicted selection preference better than seed novelty. We find that this is also true across elevation gradients on northeastern mountains. It should be noted that given the short distances between low elevation northern hardwood and high elevation spruce-fir forests, northern hardwood seeds may not be novel to the resident small mammal community at high elevation if their home ranges extend to lower elevations, however, empirical relationships between mammal body weight and home range size would indicate that the foraging area for individual small mammals (compared to herbivore mammals in general) is quite small (< 1 ha for our study species, Harestad and Bunnel 1979). Thus, individuals may experience novelty to some seed species.

Supporting H2, although seed traits were assessed qualitatively, we find that seed selection probability was generally higher for seed species with greater seed mass and nutrient reward (by protein, lipid, and carbohydrate content) as seen in other experiments (Boone and Mortelliti 2019; Mortelliti et al. 2019; Sundaram et al. 2018; Evans et al. 2020). This makes sense for the least preferred seed species, yellow birch and balsam fir, which have a small mean mass and nutrient content and are known to experience very little granivore pressure in northern forests unless as a last resort option (Duchesne et al. 2000; Lobo et al. 2013; Ogawa et al. 2017). The exception to this pattern is red spruce which had the smallest calculated mean mass per seed in this study but were as likely to be selected by small mammals as American beech, with the largest seed mass. Previous studies have shown that selection preference for spruce seeds is greater than for other conifers, particularly balsam fir, which has high levels of secondary compounds (Abbott and Hart 1960; Greenwood et al. 2008; Lobo et al. 2009; Lobo 2013; Lobo et al. 2014). Red spruce seed had some of the largest values for protein and fat content out of the seeds examined in this study, contributing to an energy content per mass of seed (kcal/g) on par with other seed species. However, given its small seed mass, granivores would need to consume more seeds to gain an energy benefit comparable to other seed species.

Our data show that average handling time for individual red spruce seeds was much lower than for other species. Thus, while granivores spent more time to process a smaller number of beechnuts, others processed a large number of small red spruce seeds very quickly. These two approaches may represent two distinct successful strategies for nutrient acquisition predicted by optimal foraging theory, where large seeds may be preferred up to the point where increased handling time increases predation risk beyond some threshold (Dylewski et al. 2020; Lichti et al. 2017; Pyke et al. 1977; Wang et al. 2013). Recent research suggests that the choice of foraging strategy could even be partly attributed to an individual animals' personality (Boone et al. 2022; Dammhahn et al. 2022). Thus, quickly processing large amounts of smaller red spruce seed may have the benefit of decreasing predation risk.

Contrary to H3, there was not a large effect of temperature, rain, or vegetation type (habitat) on seed selection preferences but a greater magnitude of effect from illumination level in our top model. We found a small decrease in probability of selection for yellow birch and American beech and a moderate increase in selection for sugar maple under increasing light levels. Previous work has observed species specific foraging behavior modulated by illumination levels in relation to perceived risk of predation (Orrock et al. 2004). Thus, a decrease in selection for seeds, especially large-seeded American beech, under increased light would reflect a predator avoidance strategy. The high uncertainty in these relationships could be caused by unmeasured confounding factors such as variable cloud cover. Perea et al. (2011) found that nighttime illumination levels more strongly affected foraging occurring in open microsites than closed ones. Additionally, Jacob et al. (2017) found a strong interaction between illumination, cloud cover, and vertical vegetative cover on seed foraging behavior of *Peromyscus leucopus*. Indeed, our study was conducted under dense forest canopy and consistent understory cover. The increased cover our study sites would likely reduce the perceived risk of predation under brighter nighttime conditions (as most seed predation events occurred at night), thus marginalizing the influence of illumination on seed selection.

Immediate or delayed consumption of post-dispersed seed serves to limit establishment potential of trees at or beyond their range margin (Brown and Vellend 2014). Conversely, seed caching behavior, particularly scatter-hoarding behaviors exhibited by *Peromyscus* species, is a positive interaction that can act to increase germination success by increasing dispersal distances and placing seeds in environmentally advantageous "safe sites" (Grubb 1977; Vander Wall 2010; Zwolak and Crone 2012; Godó et al. 2022). Supporting H4, our seed dispersal study suggests, at least for American beech, that immediate consumption was more likely to occur than seed removal and caching at all elevations. Of the seeds that were removed and cached, they were not dispersed beyond 11 m and there was no difference in seed caching substrate. While the dispersal and survival of even small numbers of seeds can lead to successful seedling establishment, high consumption or short dispersal distances dramatically decreases the probability of these outcomes, and could slow the rate of species expansion (Godó et al. 2022). Caution should be used when interpreting these results as not all tagged seeds could be recovered, and this could indicate that other seeds were dispersed greater distances or cached somewhere inaccessible. We also acknowledge that even in systems where most seeds, even cached seeds, are consumed, granivore-seed interactions can be a net positive for plant establishment (Mittelman et al. 2021). Additionally, since only beechnuts were large enough to be tagged, we cannot speculate on any differences between possible consumption vs caching behavior for other dominant tree species examined in this study. However, even assuming all missing beechnuts were cached, consumed seeds would still represent the majority of tagged seeds. This runs counter to other studies which show equivalent likelihoods of consumption and caching behavior, particularly in the fall when mammal hoarding behavior is more pronounced (Mortelliti et al. 2019). This may be the result of a handling time—predation risk trade-off, however, more studies spanning multiple seasons would be useful in determining the temporal component of seed fate.

Conclusions

The lag between the velocity of climatic change and velocity of tree range expansions may be caused by biotic interactions that serve to impede seedling establishment (Alexander et al. 2018; Zhu et al. 2012). Herbivore-plant relationships are likely one of these influencing interactions. In some studies, this inhibition of tree range changes has been referred to as a "cooling" effect (Fisichelli et al. 2012). Preferential granivory by small mammals is one obvious example of this phenomenon. This study provides evidence of high to intermediate preference of two larger seeded, dominant low elevation northern hardwood species across a gradient of elevation. While this pattern of preference did not change across different elevations, and hardwood seed preference was similar to that of red spruce, high preference in spruce-fir forests where hardwood seeds are far less abundant than conifer seeds would serve to limit the germination rate of these hardwood species, and hence, have a "cooling" effect on tree range dynamics. This is especially true when coupled with a significantly higher risk of consumption rather than beneficial seed caching. The observed patterns of seed preference may have profound implications for the future recruitment of regionally dominant tree species and for future forest composition. Future forest tree species distribution models should endeavor to incorporate information on plant-animal interactions to better estimate the potential of species to keep pace with climate change. The success of forest modeling and management efforts will depend largely on the ability to recognize and appreciate establishment filters, especially in an era of increasing global change.

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Author contributions JT conceived the ideas and methodology for this study; JT analysed the data and wrote the manuscript with substantial input from MD.; Data were collected by JT; both authors contributed to editing manuscript drafts and gave final approval for publication.

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Declarations

Competing interests The authors declare no competing interests.

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