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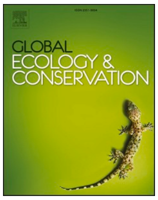

Original research article

Over the limit: Consequences of gray squirrel personality on the shifting range limits of oak and hickory species

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ABSTRACT

Many trees must shift their ranges to track changing climate conditions, but their movement often depends on animal dispersers, which are overlooked in range shift predictions. We addressed this knowledge gap by assessing the dispersal of novel (i.e., not previously encountered) seeds by gray squirrels (*Sciurus carolinensis*) and analyzing intraspecific variation in dispersal decisions. We established a field experiment spanning the northern range limits of multiple oak (*Quercus*) and hickory (*Carya*) species in Northeastern USA and measured personality of 222 squirrels, further recording seed decisions by 50 individuals. Squirrels dispersed novel seeds, illustrating their critical role in tree range shifts, with sociality and weight mediating decisions. Seed novelty mediated certain decisions such as the consumption of removed seeds, while other decisions were consistent regardless of novelty. Overall, individuals contributed to novel seed dispersal differently based on personality, highlighting the need to preserve behavioral diversity to facilitate tree range shifts.

1. Introduction

Species are shifting ranges to track suitable conditions in response to climate change (Parmesan and Yohe, 2003), with 59 % of over 26,000 recorded range shifts across taxa directionally consistent with climate change (Lawlor et al., 2024). However, species with low dispersal ability and long lifespans, such as trees, may be unable to keep pace with climate change (IPCC, 2022). In fact, plant migration projections estimate necessary shifts of 300–500 km per century, much higher than common historical rates of 20–40 km per century (Davis and Shaw, 2001). However, current predictions of plant range shifts rely on environmental and climatic conditions (McKenney et al., 2011), often ignoring the role of seed-dispersing animals, despite over 75 % of tropical trees and 30–40 % of temperate trees depending on animals for seed dispersal (Neuschulz et al., 2016). This missing piece of biotic interactions may explain why many plants are not migrating in line with temperature-based expectations (Sittaro et al., 2017; Tourville and Dovciak, 2023; Zhu et al., 2012). We simply cannot predict range shifts of trees relying on animals for seed dispersal without considering the animals responsible for moving their seeds.

One mechanism of animal-mediated seed dispersal important for large-seeded species is scatter-hoarding, or the storage of seeds in many dispersed caches for later consumption (Gómez et al., 2019). Scatter-hoarding animals, such as small mammals, act as both seed predators, eating and killing many of the seeds they encounter, and dispersers, beneficially transporting and caching seeds, falling

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somewhere on a continuum between antagonistic and mutualistic (Gómez et al., 2019). Two fundamental tree groups, the oaks (*Quercus*) and hickories (*Carya*), rely on scatter-hoarders for seed dispersal (Hurley, 1989; Steele, 2021). Oaks are found globally, with 400 + species across five continents, and both oaks and hickories play keystone roles in their ecosystems (Fralish, 2004; Steele, 2021). The loss or contraction of these species' ranges due to climate change would mean the loss of a highly consequential component of global ecosystems and a suite of ecosystem services.

For oaks and hickories to respond to the changing climate, they must rely on scatter-hoarding animals living at or near the edges of their current ranges. Animals living just inside current range limits may disperse seeds from within to outside of current ranges, into

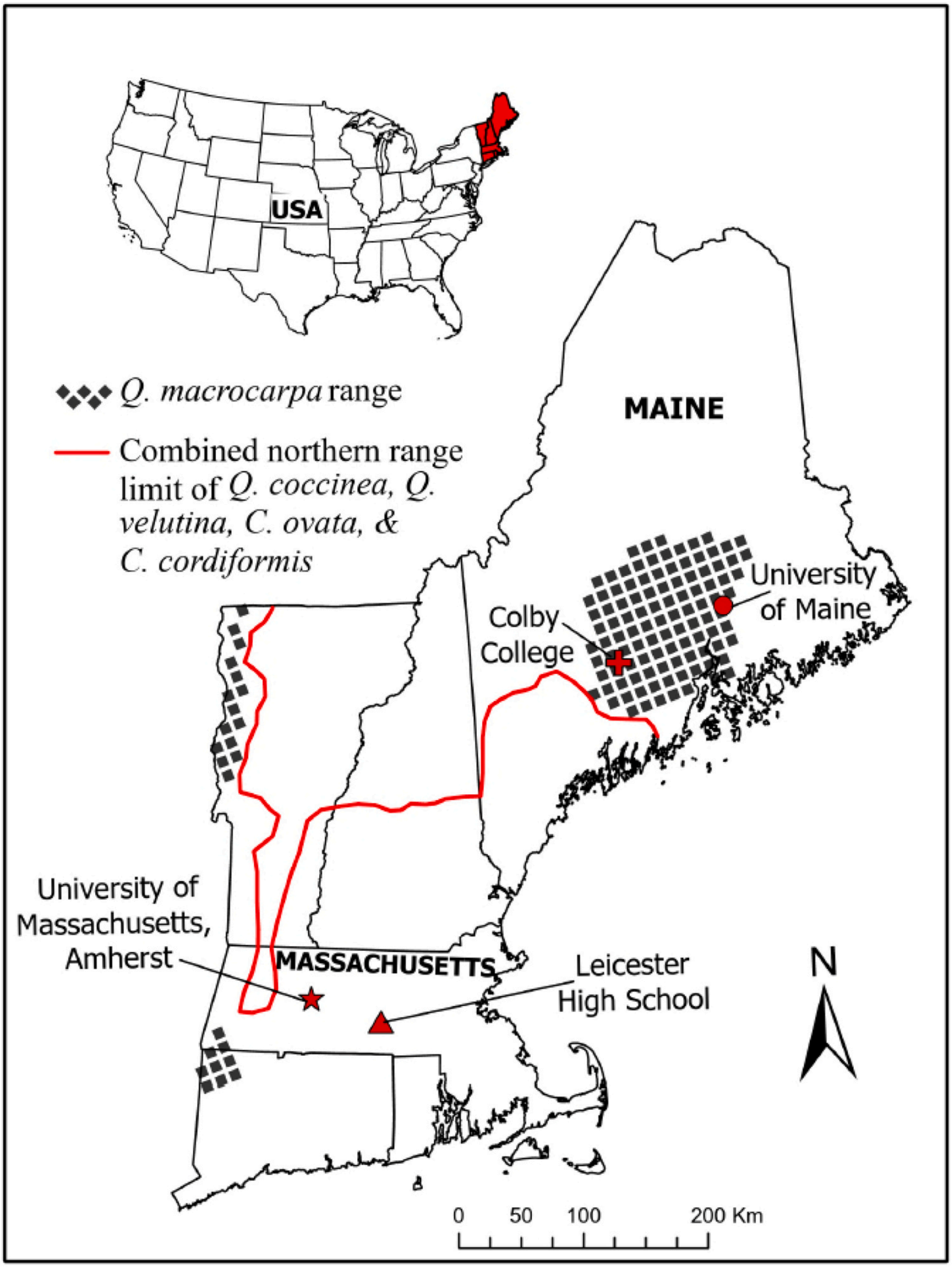

Fig. 1. This study spanned the northern range limits of multiple oak and hickory species. Red oak (*Quercus* [*Q.*] *rubra*) was familiar to squirrels throughout the study area. Scarlet oak (*Q. coccinea*), black oak (*Q. velutina*), shagbark hickory (*Carya* [*C.*] *ovata*), and bitternut hickory (*C. cordiformis*) were native to regions below the red line, thus these seeds were familiar to squirrels in Massachusetts but novel to populations in Maine. Bur oak (*Q. macrocarpa*) acorns, whose range is shown with black squares, were familiar to Maine squirrels but novel to those in Massachusetts. Note: Data about the ranges of *C. ovata* and *cordiformis* are from BGCI & IUCN (2018) and data about the ranges of *Q. coccinea*, *velutina*, and *macrocarpa* are from USGS (1999).

novel habitat. Additionally, as ranges expand, animals which live just beyond current oak and hickory range limits and which are currently unfamiliar with their seeds will encounter those seeds and decide whether to consume or disperse the novel seeds, how far to disperse seeds, and where to cache them, determining the movement and survival of the tree species (Wang et al., 2013). We know that small mammals interact with novel seeds, with seed traits dictating their decisions (Mortelliti et al., 2019). Additionally, the personality, or consistent individual behavioral type (Sih et al., 2004), of mice and voles influences their seed dispersal decisions (Boone et al., 2021; Brehm et al., 2019; Merz et al., 2023). To predict plant range shifts and conserve the seed dispersal process, we must consider individual differences in seed-dispersing animals (Hunter et al., 2021; Mortelliti, 2023) because certain individuals may play a disproportionate role, becoming 'keystone seed dispersers' that must be conserved because they cannot be replaced (Zwolak and Sih, 2020). However, to the best of our knowledge, no study has yet looked at how disperser personality and seed novelty interact to mediate seed dispersing decisions.

To fill this gap, we designed a large-scale field experiment focusing on the longstanding relationship between eastern gray squirrels (*Sciurus carolinensis*) and oak and hickory seeds (Barnett, 1977; Steele, 2021) and spanning the northern range limits of multiple oak and hickory species (Fig. 1). We compared squirrel seed interactions between populations that are familiar with the seeds we offered and populations that are unfamiliar with those seeds, but expected to encounter them in coming years due to changing conditions (Peters et al., 2020). With this design, we assessed: 1.) squirrel selection and dispersal of novel seeds, including the probability to remove seeds, dispersal distance, consumption of removed seeds, and mutualistic (i.e., dispersal with possible germination) tendency, 2.) whether squirrel personality influences seed decisions, and 3.) whether squirrel personality interacts with seed novelty to mediate decisions.

We predicted that squirrels would disperse novel seeds, preferring harder and less perishable seeds regardless of novelty and dispersing these seeds farther and burying them for a mutualistic outcome (Hadj-Chikh et al., 1996; Mortelliti et al., 2019; Steele and Yi, 2020). We also predicted that bolder squirrels and those with better stress-coping ability would select harder and larger seeds more often despite the increased risk caused by longer handling times and that bolder and more active squirrels would eat seeds more often, but, when dispersing them, disperse seeds farther (Brehm et al., 2019, Brehm and Mortelliti, 2022). Lastly, we predicted that personality would mediate squirrels' interactions with novel seeds more than interactions with familiar seeds. The risk of interacting with,

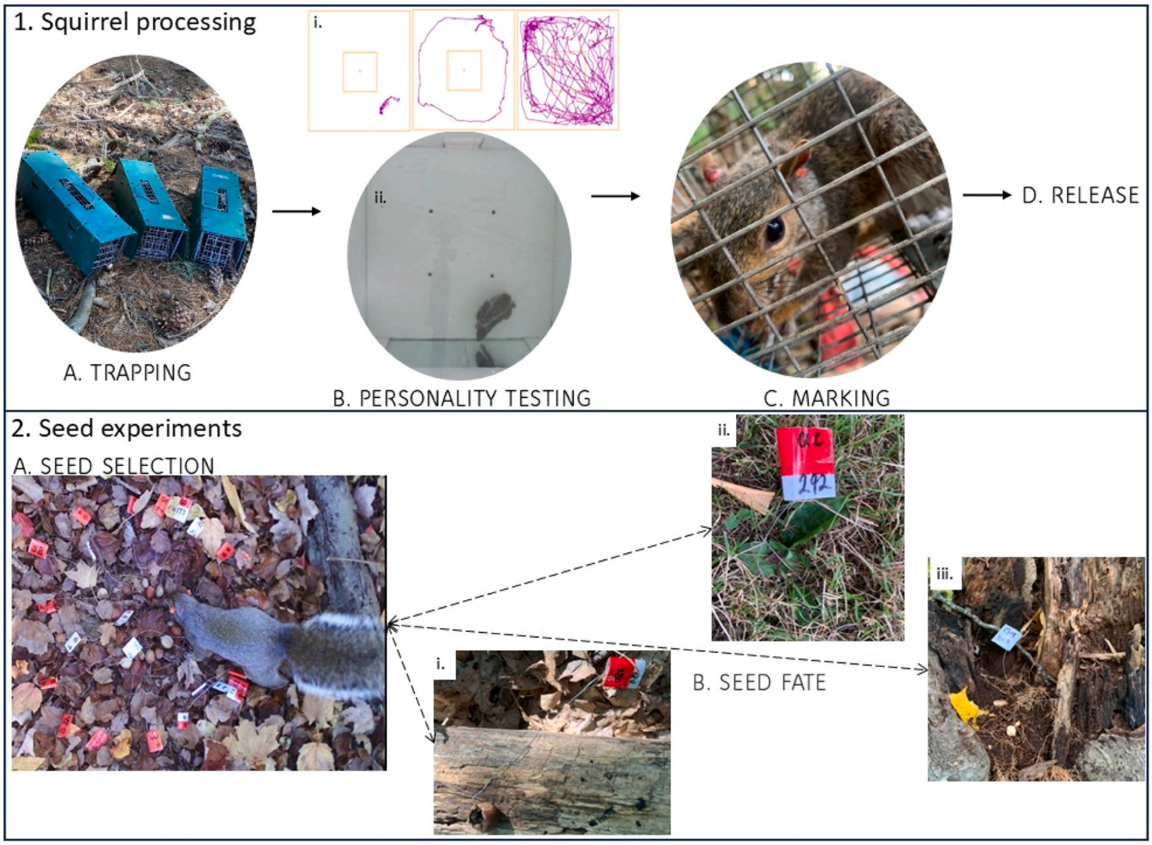

Fig. 2. An overview of our experimental design. At field sites, we 1 A.) trapped squirrels, 1B.) assayed their behavior with i.) an open-field test (three ANYMaze tracks shown), ii.) a mirror test, and a handling bag test (not shown), 1 C.) marked them with ear tags and haircuts, and 1D.) released them at their site of capture. We then conducted seed dispersal experiments, 2 A.) using trail cameras to record squirrel seed selection and 2B.) flags on seeds to record seed dispersal fate as ignored, eaten at the station, or dispersed and i.) partially consumed, ii.) cached intact, or iii.) fully consumed.

and the lack of information about, a new resource may cause differences in individual foraging decisions, while reliable information about known resources results in consistent foraging decisions (Carter et al., 2013). Overall, we expected that certain gray squirrels, based on their personality, would be more consequential in impeding or facilitating oak and hickory climate-driven range shifts.

2. Methods

2.1. Study area

We trapped and assayed squirrel behavior in the states of Maine, Massachusetts, Rhode Island, and New Hampshire in Northeastern USA. Due to low capture numbers and difficulty getting tagged individuals to visit seed stations, after an initial pilot season, we focused our efforts for the seed dispersal experiments on sites in Maine and Massachusetts. Thus, the squirrels included in behavioral analyses and seed dispersal experiments were exclusively from sites in Maine and Massachusetts (Fig. 1). We established two seed dispersal experiment sites in Massachusetts, at the University of Massachusetts Amherst (Amherst, MA) and Leicester High School (Leicester, MA), and two in Maine, at the University of Maine (Orono, ME) and Colby College (Waterville, ME). We chose to work on university and high school campuses because of high gray squirrel abundances and because it allowed us to assess squirrels' dispersal behavior in suburban areas, areas of concern for trees' ability to migrate (Han and Keeffe, 2021).

2.2. Squirrel processing

Squirrel trapping was conducted from 2020 to 2022 at the University of Maine, in 2022 at Colby College, Leicester High School, and the University of Massachusetts, and for one year between 2020 and 2022 at all other field sites. We trapped opportunistically between June and November, setting 20–60 Tomahawk traps (Tomahawk Live Trap Co., WI, USA; Model 102XL) baited with peanut butter and/or sunflower seeds. We set traps in the morning facing large trees likely or visibly used by squirrels and checked them in the afternoon. Squirrel trapping was part of a coordinated citizen science effort with students from the schools we worked at helping to set and check traps and learning about the behavioral assays we use to measure personality.

We ran three behavioral assays on captured gray squirrels: the open-field test (OFT) for activity and exploration (Mazzamuto et al., 2018), the mirror-image stimulation (MIS) test for aggression and sociality (Mazzamuto et al., 2018), and the handling bag test for docility (Martin and Réale, 2008). We transferred squirrels from their trap of capture into a clean 79x79x79cm white arena with a clear plexiglass top for the OFT and used a camera (Canon, Tokyo, Japan; PowerShot Elph 180 digital camera) to record their behavior from above for 5 minutes. Then, we slid open one side of the arena, revealing a mirror, and recorded animals for a 2.5-minute MIS test (Fig. 2). Lastly, squirrels were transferred into a cloth bag and held still for 1 minute while we recorded the number of seconds the squirrel was immobile as a measure of docility.

Next, we marked squirrels with two metal ear tags (National Band and Tag Company) affixed with colored wire and pipe cleaners for visual identification (Video S1). We gave squirrels unique body and tail haircuts (Video S1), recorded their sex and weight, and then released them at their site of capture.

Lastly, we watched the OFT and MIS test videos, using the software ANY-maze© (version 5.1; Stoelting CO, USA) to record the amount of time squirrels spent grooming (a measure of stress-coping ability), their mean speed (a measure of activity), number of rears (i.e., two front paws lifted off the ground; measure of exploration), and amount of time spent in the center of the OFT arena (a measure of boldness; Fig. 2) and the amount of time spent socially interacting with the mirror (i.e., sniffing or touching the mirror in a non-aggressive stance; a measure of sociality) in the MIS test (Mazzamuto et al., 2018). We ran repeatability analyses on behavioral variables, considering variables with significant repeatability estimates as personality and only moving forward with repeatable traits in further analyses. Although behavioral traits can exhibit plasticity, which is an important aspect of behavior that may determine foraging behavior, in this paper, we focused on the role of personality, or traits that are consistent across time and context (Réale et al., 2010), selecting to only move forward with significantly repeatable traits representing personality. We obtained one unique personality measure per individual per trait and checked correlations among personality variables, moving forward only with non-correlated traits. For details on repeatability analyses and for a table of repeatability estimates see Appendix S1.

2.3. Seed experiments

We conducted seed experiments in 2020 and 2022 at the University of Maine and in 2022 at Colby College, Leicester High School, and the University of Massachusetts between August and November. We focused on large-seeded hardwood species that rely on squirrels for dispersal, selecting seeds from the oak and hickory families. First, we selected a reference seed native to squirrels at all sites, the northern red oak (*Quercus rubra*). Then, we chose seeds that were familiar to squirrels in Massachusetts and novel to Maine populations based on their native ranges, but with ranges expected to overlap Maine sites in the future based on predicted climate conditions (Peters et al., 2020), selecting the scarlet oak (*Quercus coccinea*), black oak (*Quercus velutina*), shagbark hickory (*Carya ovata*), and bitternut hickory (*Carya cordiformis*) (BGCI and IUCN, 2018; USGS, 1999). Lastly, we selected a seed that was native at Maine sites but novel to squirrels in Massachusetts, the bur oak (*Quercus macrocarpa*; USGS, 1999), to ensure that at every site, squirrels had the choice of a novel and native seed. With this design, although the seeds we used had a range of traits, seeds were offered as native to some squirrels and novel to others, ensuring that overall selection of novel versus native seeds was not confounded by seed trait differences. The only seed not included as both native and novel was the red oak, which was included as a reference seed due to its familiarity to all squirrels in this study.

We tagged seeds by threading thin beading wire through the top of them and attaching a reflective tag, with an alphanumeric code for identification, to the wire to aid in relocating dispersed seeds (Fig. 2). This method of seed tagging does not impact squirrel seed selection or whether they eat or disperse seeds (Xiao et al., 2006). We set out four seeds of each species at each site, placing them directly on the ground either in a circle (Fig. 2) or in rows, at the base of trees on which we could mount trail cameras. We used motion-activated trail cameras (Bushnell NatureView Cam HD) set to record 60-second videos to monitor squirrel seed selection (Fig. 2; Video S1). We set seed stations in the morning and checked them once in the afternoon, removing all equipment after checking.

Upon checking stations, we recorded whether seeds found at the station were consumed, partially consumed, or left intact. We then used flashlights to search for the reflective tags on removed seeds, estimated the distance seeds were dispersed in meters (Video S2), and recorded whether they were consumed, partially consumed, or cached intact (Fig. 2). We noted the location of dispersed seeds as being either up a tree or on the ground, either at the base of a tree, in the open, or under or next to woody debris.

Finally, we analyzed trail camera videos and recorded which squirrels visited stations (identified by ear tags and haircuts), which seeds they selected, whether they consumed seeds at the station or removed them, and the seed availability at the time of a visit (i.e., we counted the number of seeds of each species available for selection in the video footage, Video S1). Combining the field dispersal data and the video analysis, we linked the selection and dispersal fate of seeds to squirrels with known personalities (Brehm et al., 2019; Brehm and Mortelliti, 2022).

2.4. Seed selection analysis

We ran multinomial mixed-effect models to analyze seed selection, with the seed species selected as the categorical response variable, the availabilities of each seed species at the time of selection as fixed effects, and squirrel ID as a random effect (Boone and Mortelliti, 2019; Koster and McElreath, 2017; Mortelliti et al., 2019). We ran models using the 'rethinking' (McElreath, 2020) and 'Rstan' (Stan Development Team, 2024) packages in R, using methods from Koster and McElreath (2017). We provided weakly informative priors for the fixed effect parameters and variance-covariance matrices. Priors prevented highly implausible values, but otherwise assumed that zero represented the highest probability for parameters (Koster and McElreath, 2017). We ran 1000 warm-up iterations and then three chains each containing 2000 iterations (Koster and McElreath, 2017). We first ran models including all six seed species, testing the effects of squirrel sex, weight, range (i.e., Massachusetts or Maine), personality, and an interaction between personality and range as fixed effects against a null model. We compared models using the widely applicable information criterion (WAIC). For any models ranking within 2ΔWAIC of the top model, we tested an additive model including all variables from these top models and selected a final model if it was more than 2ΔWAIC above non-additive models. We assessed the traceplots, n_eff (i.e., number of effective samples), and Gelman-Rubin convergence diagnostic ($Rhat<1.1$) of top models to evaluate convergence and mixing of chains (McElreath, 2020). We made inferences about selection based on the probability of selection with 89 % percentile intervals calculated from the posterior samples of the top model (see McElreath, 2020 for an explanation of the 89 % percentile intervals).

Next, we ran the same models as above, but included novelty (a binomial variable describing each seed selection as either a novel or familiar interaction for the squirrel) to assess whether novelty influences selection. We were unable to include novelty previously because it was impossible to have a novel interaction with a red oak acorn. Thus, for this analysis, we removed selections of red oak. We still included red oak availability as a fixed effect as well as availabilities of all other seed species at the station, squirrel ID as a random effect, and we tested the effects of squirrel range, sex, weight, personality, seed novelty, and interactions between personality and both squirrel range and seed novelty. We followed the same methods as above for selecting and checking a top model and for making inferences.

2.5. Seed dispersal analysis

To analyze dispersal outcomes, we opted not to use multi-response Bayesian models because of the computational costs of those models when incorporating as many predictor variables as we felt may influence our response variables and because of the number of models needed to assess the importance of those predictors. We could do more exploration of predictor variables while running fewer models using linear mixed-effect models. We ran models using the 'lme4' package (Bates et al., 2015) in R and removed interactions that ended in rejection at the station (Video S1; see Appendix S2 for a supplementary analysis assessing the probability of a seed interaction ending in rejection). We first ran generalized linear mixed-effect models with a binomial distribution to assess the probability of a squirrel removing versus immediately consuming a seed. Second, we assessed dispersal distance, including seeds buried at the station so a dispersal distance of 0 m is possible, but only including seeds that were selected and not eaten because eaten seeds are not dispersed in a beneficial way for the tree. We used a Box-Cox (Box and Cox, 1964) transformation on the dispersal distance to approximate normality and ran linear mixed-effect models. Third, we assessed the probability that a squirrel ate a removed seed, only considering seeds that were dispersed away from the station, and ran models with a binomial distribution. Lastly, we ran the same type of model to assess the probability that an interaction ended with a mutualistic outcome for the seed. We removed interactions with the bur oak for this analysis because there were no mutualistic interactions with bur oaks. We considered seeds buried intact or dispersed away from stations and left on the surface uneaten as mutualistic outcomes, as long they were not up a tree or left on stone surfaces.

We used a build-up model selection process to determine a top model for each response variable, first testing the effects of seed species, seed novelty, squirrel range, and field site against a null model. We moved forward with the top model from this set if it ranked more than 2Δ Akaike information criterion (AIC) above the null model and we tested an additive model including all variables in models that ranked above the null and within 2ΔAIC of the top model. We used the top model from this set as the null model for the subsequent set, testing the effects of squirrel sex and weight and repeated the same process as above. We continued in this way through the last three model sets, testing the effects of personality and interactions between personality and both seed species and novelty. We scaled all numeric predictor variables before including them in models and made inferences from the final top model.

3. Results

3.1. Behavioral analysis

We assayed the behavior of 222 gray squirrels (262 observations; Appendix S1 Table S1). Four behavioral variables were significantly repeatable (mean=0.55, range=0.46–0.70; Appendix S1), including mean speed, proportion time in the center, and proportion time grooming in the OFT and proportion time socially interacting with the mirror in the MIS test, while rear rate and handling score were not repeatable and thus not used in subsequent analyses (Appendix S1). We moved forward with the repeatable traits, except for mean speed because it was moderately correlated with time spent in the center of the OFT ($r = 0.56$) and grooming ($r = 0.42$; Appendix S1).

3.2. Seed experiments

Over the two years, we established 139 seed stations and set 3256 seeds in the field. We recorded 638 seed interactions by 50 squirrels with known personality (Video S1). Of those, 508 were seed selections by 50 squirrels, excluding interactions where squirrels rejected seeds or their action was unknown due to video quality or length (see Appendix S2 for a supplementary analysis assessing the probability of a seed interaction ending in rejection from the 99 rejection events we recorded). From seed searching, we found 330 dispersed seeds (i.e., selected but uneaten). Of those, 98 were dispersed by 24 squirrels of known personality an average of 9.78 m

Table 1

Results for the linear mixed-effects models analyzing seed dispersal and the multinomial mixed-effects models analyzing seed selection. Model ranking was done using AIC (Akaike information criterion) for the seed dispersal models and WAIC (widely applicable information criterion) for seed selection models. Models < 2 Δ(W)AIC from the top-ranked model are shown. Bolded predictor variables have confidence intervals not overlapping zero. R^2c is the conditional R-squared value and R^2m is the marginal R-squared value. Beta estimates and R^2 values are not applicable to the multinomial models of seed selection. CC = bitternut hickory (*Carya cordiformis)*, CO = shagbark hickory (*Carya ovata),* QC = scarlet oak (*Quercus coccinea*), QM = bur oak (*Quercus macrocarpa*), QR = red oak (*Quercus rubra*), and QV = black oak (*Quercus velutina*).

Response Variable	**Model Predictor Variables ($\widehat{\beta} \pm SE$)**	**Δ(W) AIC**	**Cumulative (W)AIC Weight**	**R^2c (R^2m)**
Dispersal distance	**Seed species** (CO:−0.01±0.38, **QC:−2.50±0.69, QM:−3.22±*1.03***, QR:−0.92±0.48, **QV:−1.99±0.48)** + **Intercept (2.39±0.57)**	0.0	0.56	0.77 (0.13)
	Sex (Male:−0.76 ± 0.99) + **Seed species** (CO:−0.01 ± 0.38, **QC:−2.46 ± 0.70, QM:−3.11 ± 1.04**, QR:−0.88 ± 0.48, **QV:−1.99 ± 0.48**) + **Intercept (2.83 ± 0.80)**	1.85	0.79	0.77 (0.15)
	Proportion time grooming (−0.36±0.51) + **Seed species** (CO:−0.001±0.38, **QC:−2.52±0.69, QM:−3.18±*1.03*, QR:−0.95±0.48, QV:−2.00±0.48)** + **Intercept (2.41±0.56)**	1.92	1.0	0.77 (0.14)
Probability of removing or immediately consuming a seed	**Seed species** (CO:0.49±0.52, **QC:−2.87±0.54, QM:−4.91±0.63, QR:−1.42±0.47, QV:−2.06±0.47**) + **Intercept (2.63±0.46)**	0.0	0.35	0.64 (0.34)
	Proportion time center (−0.38±0.29) + Seed species (CO:0.49±0.52, **QC:−2.89±0.54, QM:−4.95±0.63, QR:−1.41±0.47, QV:−2.07±0.47)** + **Intercept (2.63±0.46)**	0.29	0.66	0.64 (0.35)
	Sex (Male:0.52±0.58) + Seed species (CO:0.50±0.52, **QC:−2.85±0.54, QM:−4.87±0.63, QR:−1.42±0.47, QV:−2.05±0.47)** + **Intercept (2.36±0.54)**	1.27	0.84	0.64 (0.36)
	Proportion time grooming (−0.20±0.29) + Seed species (CO:0.49±0.52, **QC:−2.86±0.54, QM:−4.92±0.63, QR:−1.42±0.47, QV:−2.06±0.47)** + **Intercept (2.61±0.46)**	1.61	1.00	0.64 (0.34)
Probability of eating a removed seed	Novelty (−0.17±0.47) * **Sociality (−0.64±0.31; Interaction term:1.78±0.56)** + **Weight (−0.71±0.30)** + **Intercept (0.51±0.36)**	0.0	1.00	0.39 (0.25)
Probability of a mutualistic outcome	Sociality (−0.27±0.58) *Seed species (CO:0.95±0.49, **QC:−5.91±*2.72***, QR:−0.56±0.55, **QV:−1.21±0.54;** Interaction terms: CO:0.40±0.58, **QC:−76.62±3.28,** QR:0.83±0.67, QV:0.08±0.66) + **Weight (0.93±0.40)** + **Intercept (−1.87±0.58)**	0.0	1.00	0.83 (0.70)
Seed selection	**Analysis** **All seed species** (novelty not included) Sociality	0.0	0.40	NA
	Range	0.60	0.79	NA
	Not including red oak (novelty included) Sociality*Novelty	0.0	0.65	NA

(range=0–65.79 m).

3.3. Seed selection

The top model for seed selection included sociality (Table 1). Squirrel sociality affected seed selection in different directions and with different strengths depending on the seed species and seed availability (Appendix S3; Figure S1). Squirrels preferred hickory seeds regardless of which population they were from (Fig. 3).

The top model predicting seed selection from the analysis that excluded red oak in order to assess the effects of novelty included an interaction between squirrel sociality and seed novelty (Table 1). This model also indicated preference for hickories regardless of novelty and a variable effect of squirrel sociality on seed selection based on seed species and availability (Appendix S3; Figure S2).

3.4. Seed dispersal

For the probability of removing a seed, we had 508 selections from 50 squirrels and the top model included seed species (Table 1). Hickory nuts were more likely to be removed while acorns were more likely to be consumed, with the bur oak most likely to be immediately consumed (Table 1).

To assess dispersal distance, we had 98 observations from 24 squirrels and the top model included seed species with hickory seeds more likely to be dispersed farther (Table 1). Bitternut hickory seeds were dispersed the farthest (mean=11.95 m, range = 0.3–65.79 m), while bur oak acorns were dispersed the shortest distances (never dispersed away from the station) followed by scarlet oak acorns (mean=0.97 m, range = 0–5 m).

For the probability of eating a removed seed, we had 178 observations from 35 squirrels. Most removed and uneaten seeds were buried intact, but a few were left on the surface, brought up trees, or left with a cracked shell. The top model included squirrel weight and an interaction between squirrel sociality and seed novelty (Table 1). Larger squirrels were less likely to consume seeds, and more social squirrels were more likely to eat removed novel seeds while being less likely to eat removed native seeds (Fig. 4).

For the probability of a mutualistic outcome, we had 328 observations from 47 squirrels. The top model included squirrel weight,

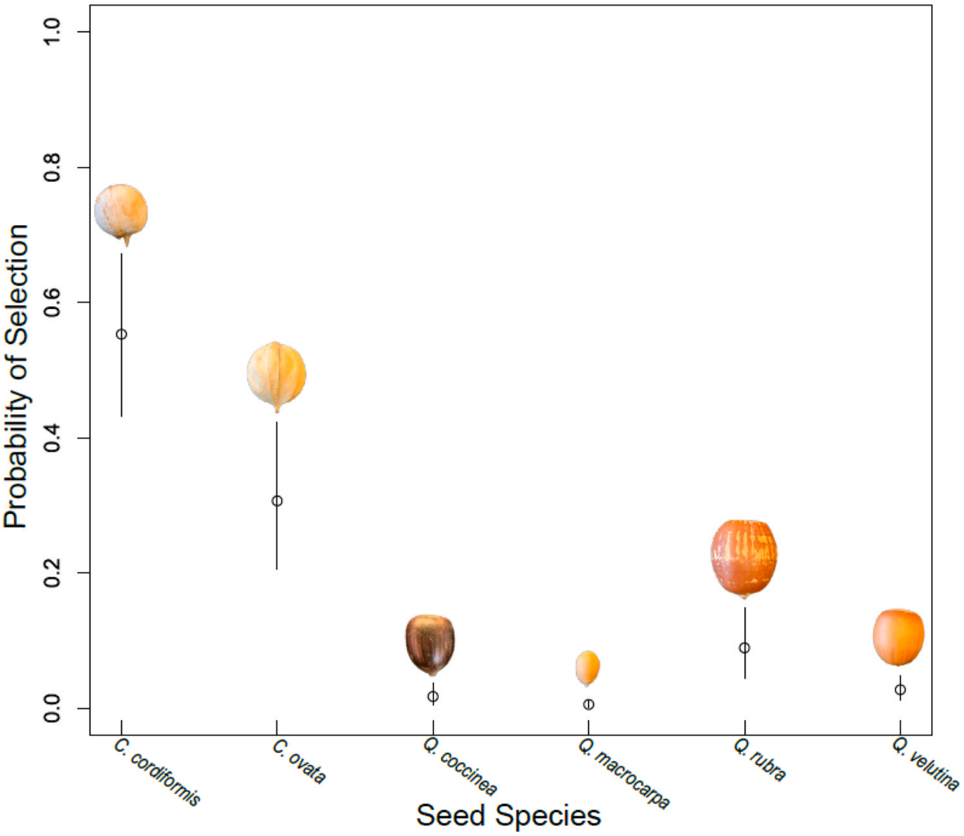

Fig. 3. Gray squirrels were more likely to select hickory seeds than acorns. Predictions of squirrel seed selection are based on the top-ranked multinomial model from the seed selection analyses, which includes squirrel sociality. Estimates are shown with 89 % percentile intervals calculated from the posterior samples of the top model. Note: *C.* = *Carya, Q.* = *Quercus*. *C. cordiformis* = bitternut hickory, *C. ovata* = shagbark hickory, *Q. coccinea* = scarlet oak, *Q. macrocarpa* = bur oak, *Q. rubra* = red oak, and *Q. velutina* = black oak.

with heavier squirrels more likely to be mutualistic (Fig. 4), and an interaction between squirrel sociality and seed species, with squirrel sociality affecting mutualistic outcome differently depending on the seed species (Table 1).

4. Discussion

Through a large-scale field experiment, we found that gray squirrels' role in seed dispersal varies individually, with sociality and body weight influencing seed caching decisions. Additionally, gray squirrels readily interacted with novel seeds, with novelty influencing the probability of eating a removed seed and specific seed selection probabilities, while other seed caching decisions remained consistent regardless of novelty. Squirrels' willingness to disperse novel seeds highlights their important role in climate-driven tree range shifts, while both seed and squirrel traits mediate whether that role is positive or negative.

4.1. Individual squirrel traits

Sociality mediated seed selection, probability of eating removed seeds, and mutualistic tendency. More social squirrels were more likely to consume novel seeds while being less likely to consume native seeds once seeds were removed from a station (Fig. 4). To our knowledge, this is the first study looking at the effects of sociality on seed dispersal, an important extension of work exploring the impacts of social environment on squirrel caching behavior. In the presence of conspecifics, gray squirrels alter their foraging and caching behavior to minimize competition and pilferage (Hopewell and Leaver, 2008; Steele et al., 2008). Interestingly, squirrels' sociality may mediate the amount of competition they face, as squirrels in urban areas are more social than those in suburban areas, potentially due to higher competition (Tranquillo et al., 2024). This result may also suggest an advantage of sociality for adapting to novel habitats and resources, such as those in urban areas. Thus, more social squirrels may be more likely to consume novel seeds due to sociality enhancing squirrels' ability to adapt to and exploit novel resources, in line with findings that urban areas had more social squirrels, or due to the potential increased competition faced by social squirrels causing behaviors, such as consuming seeds, that limit pilferage. Consequently, in areas with denser squirrel populations, the consumption of novel seeds could be greater, inhibiting dispersal and range expansion. Competition may also explain why the effects of sociality on seed selection and mutualistic tendency depended on seed species (Table 1), as increased pressure on high quality resources could alter the relative quality of seeds. This result may be an interaction between seed quality and sociality mediated by competition. For example, at low seed availability, more social squirrels were more likely to select bur oak acorns, the least preferred seed, than less social squirrels (Appendix S3; Figure S1), potentially because more social squirrels face increased competition, under which conditions highly preferred seeds may have been selected more quickly leaving only the lesser preferred seeds as a resource.

Gray squirrels' social system lies somewhere between solitary and group-living, but dominance hierarchies do exist, with dominant squirrels capable of monopolizing food patches (Koprowski, 1994; Thompson, 1978). Currently, it is unknown how sociality measured in the MIS test correlates to social status (Santicchia et al., 2020). Thus, more work remains to tease apart the effects of sociality, competition, and social rank on squirrel foraging behavior and to validate how measures of sociality in the MIS test translate to social status in free-living squirrels. Nevertheless, we must consider squirrel sociality, its interaction with seed novelty, and social context

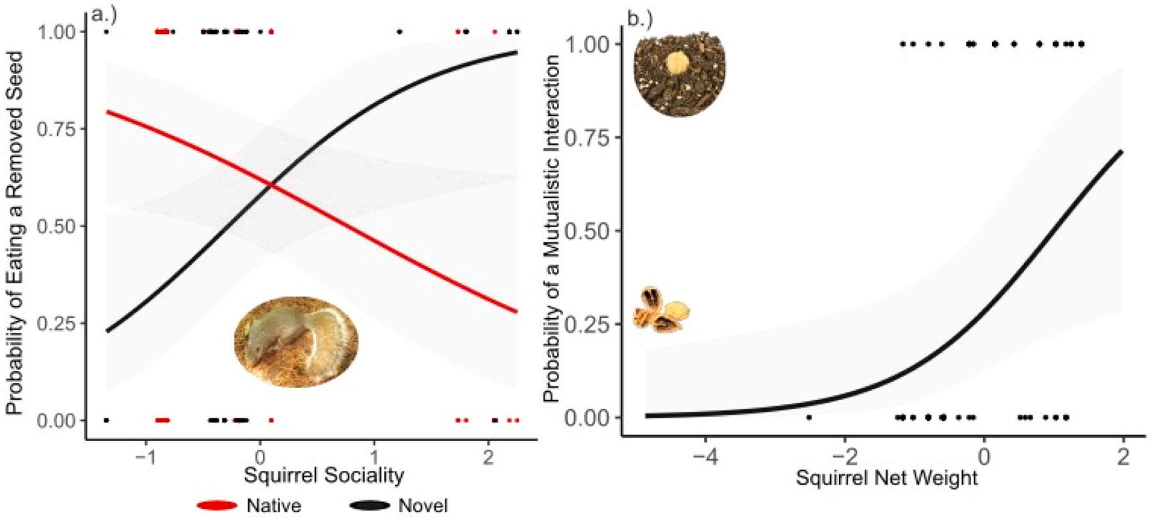

Fig. 4. a.) More social gray squirrels are more likely to eat removed novel seeds and less likely to eat removed native seeds than less social squirrels. b.) Larger gray squirrels are more likely to interact mutualistically (i.e., dispersal allowing possible germination) with seeds. Predictions from the top-ranked model are shown with 95 % confidence intervals. Predictions displayed were obtained using a.) the mean squirrel weight and b.) the mean value for squirrel sociality and for interactions with shagbark hickory seeds. Points display raw data. Net weight and sociality are scaled variables and more positive values correspond to more social squirrels.

when predicting seed dispersal outcomes.

Additionally, it should be considered that in our collection of personality data, we prioritized a month-long interval between behavioral assays to reduce squirrel habituation to tests and to strengthen our estimates of repeatability (Dingemanse and Wright, 2020). However, this limited our number of repeat assays of individuals, which is reflected in the large confidence intervals on our repeatability estimates. Yet, even with these large intervals, our estimates were significant. We emphasize that our assay numbers are in line with work on similar species (Boyer et al., 2010; Mazzamuto et al., 2018) and that we retained individuals with one observation in our estimates of repeatability as recommended (Martin et al., 2011).

Aside from personality, body weight, another individual trait, also mediated seed dispersal decisions. Heavier squirrels were less likely to eat removed seeds and more likely to have mutualistic dispersal outcomes (Fig. 4). Caching seeds costs a lot of energy, from transporting the seeds, digging caches, and remembering where caches are (Wang et al., 2013). In this context, larger individuals with more stored energy would be more likely to cache seeds, plus it may be more manageable for larger individuals to carry seeds (Muñoz and Bonal, 2008). Additionally, individuals in poor condition display higher motivation to feed (David et al., 2012; Humphreys and Mortelliti, 2024). Thus, lighter animals may consume seeds more often because the energy available from consuming a seed may be necessary for animals with less stored energy. Overall, individual seed disperser traits such as weight must be considered when predicting seed predation rates, and larger squirrels may have lower predation rates, contributing more positively to seed dispersal.

4.2. *Selection of novel seeds*

Squirrels preferred hickory nuts over acorns (Fig. 3), in line with previous findings, potentially due to higher levels of protein, crude fat, and digestible energy in hickory nuts (Cilles et al., 2016). Squirrels were also more likely to remove hickories, disperse them farther, and interact mutualistically with them, matching past studies (Cilles et al., 2016). These patterns may be due to differences in dormancy and perishability, with squirrels caching dormant and less perishable seeds, such as hickories, more than non-dormant seeds (Hadj-Chikh et al., 1996). Although we did not explicitly measure seed traits, we know that hickories tend to be larger, less perishable, have less tannins, and have harder shells than the acorns used in this study (Cilles et al., 2016; Mortelliti et al., 2019), potentially driving observed patterns. Notably, many of these patterns remained consistent whether squirrels were interacting with novel or familiar seeds, indicating that squirrels can make decisions based on seed traits with seeds that are new to them.

Overall, we demonstrate squirrels' reliance on seed traits over familiarity in making dispersal decisions (Mortelliti et al., 2019). Naive and familiar squirrels reacted similarly to the seeds in this study, suggesting that these decisions may be instinctive, complementing findings that there is an innate basis to squirrel caching decisions (Steele et al., 2006). There may be optimal caching decisions for seed species, based on their seed traits, which are not subject to individual variation. These seed traits, and squirrels' consistent decisions based on them, can be incorporated into models of seed dispersal and tree range expansion to account for the role of squirrels in these processes. Importantly, however, an interaction between sociality and novelty did influence the probability to eat removed seeds and certain seed selection probabilities, indicating that novelty is important for some decisions. While squirrel interactions with native seeds may be a useful guide when predicting some decisions with novel seeds, we must also consider how seed dispersal outcomes will change as seeds disperse to new regions. Squirrel personality is an important driver of novel seed dispersal patterns. Therefore, understanding the personality distribution of squirrels in a region can greatly enhance predictions of seed dispersal. Environmental heterogeneity and population density are both related to the diversity of personality traits in a population (Mortelliti and Brehm, 2020). These relationships, as well as known effects of land-use change, such as urbanization and forest management (Brehm et al., 2019; Tranquillo et al., 2024), on personality distributions suggests that it is potentially possible to predict the personality diversity and distributions of animal populations in new regions, which can then be incorporated into seed dispersal predictions. Further work is required to expand upon and validate such predictive work.

It should be considered that this study focused on primary seed dispersal, but cached seeds are often recached by pilferers or cache owners trying to avoid pilfering (Vander Wall, 2000). Thus, seeds may be recached, with the potential to be eaten each time, many times after initial dispersal. Accordingly, our results should be interpreted as the initial step of the seed dispersal process, not as the final fate of seeds, and future work should follow caches through multiple dispersal events and spring germination to investigate the role of squirrel personality in the final fate of seeds.

4.3. *Conservation implications*

1) *Behavioral diversity*. Due to differences in individual contribution to seed dispersal based on personality, to conserve this ecosystem service, we must conserve behavioral diversity among seed-dispersing animals (Hunter et al., 2021). Behavioral diversity is often overlooked despite its necessity for the maintenance of ecosystems (Smith and Blumstein, 2013), but it can be conserved by maintaining genetic diversity (Bubac et al., 2020), prioritizing environmental heterogeneity (Mortelliti and Brehm, 2020; Smith and Blumstein, 2013), and maintaining high population densities (Mortelliti and Brehm, 2020). The irreplaceability of 'keystone seed dispersers' emphasizes the need for behavioral diversity conservation to avoid the loss of disproportionately consequential individuals (Zwolak and Sih, 2020).
2) *Contribution to assisted migration.* Assisted migration, or the intentional movement of trees to help them track changing conditions, is a proposed tool to reduce the threat of climate change (Aubin et al., 2011). A barrier to implementing assisted migration is uncertainty about the response of transported trees to their new environments, including unknown potential biotic interactions, including seed predation and/or dispersal, after assisted migration (Aubin et al., 2011, Park and Talbot, 2012). We show that gray squirrels disperse seeds from outside of their native ranges, highlighting how squirrels may help disperse seeds of trees brought to

new areas through assisted migration. We emphasize the need to consider the animals that will interact with seeds once they are transported when predicting the outcomes of assisted migration. Specifically, areas with larger populations of social squirrels, such as urban areas (Tranquillo et al., 2024), may experience reduced success of assisted migration because squirrels will predate more of the novel seeds produced by transported trees, while populations with larger squirrels may experience more seed dispersal after assisted migration, enhancing the establishment of species in new regions.

3) *Impact in introduced regions.* Gray squirrels are a highly invasive species (Gurnell et al., 2016), and although the impacts of gray squirrels on native ecosystems have been considered (Gurnell et al., 2016) and their feeding behavior on novel food resources in introduced regions has been documented (Wauters et al., 2002, 2005, 2023). We provide further evidence that introduced squirrels will likely participate in seed dispersal in introduced regions because of their readiness to disperse novel seeds. It should be considered that invasive squirrels may form novel mutualisms with native species, dispersing their seeds, but also potentially contribute to the dispersal of invasive species, thus having impacts that are hard to predict (Case et al., 2024).

5. Conclusions

Our findings underscore the need to incorporate biotic interactions and consider individual traits such as personality in predictions about species' responses to climate change, highlighting the need to conserve behavioral diversity for the maintenance of ecosystem services (Hunter et al., 2021; Mortelliti, 2023). Gray squirrels are key players in the seed dispersal and potential range shifts of large-seeded trees (Gómez et al., 2019), and we show that squirrel interactions with native seeds may be useful for predicting their reaction to novel seeds, as many squirrel decisions remained consistent regardless of novelty. Novelty was important for certain decisions, however, so we must also consider how seed dispersal outcomes may change as seeds disperse to new regions. We also provide promising evidence that squirrels will disperse seeds into and through suburban areas (i.e., university campuses), areas of concern for trees' ability to migrate (Han and Keeffe, 2021). Due to the impact of urbanization on squirrel personality, such as increased sociality (Tranquillo et al., 2024), our findings may not be applicable to rural squirrel populations. Further work should investigate the generalizability of our results to different contexts. Overall, due to the importance of trees' ability to migrate for their continued survival in a changing climate, understanding individual dispersers' roles in novel seed dispersal processes is crucial for predicting future forest compositions.

Ethical note

Squirrel trapping and handling was conducted in accordance with our approved protocol from the University of Maine's Institutional Animal Care and Use Committee (IACUC A2018–11–02, A2021–12–01) and with the proper permits (Massachusetts Division of Fisheries and Wildlife Scientific Collection Permit #008.22SCM, Rhode Island Department of Environmental Management Division of Fish & Wildlife #2021–50-W, New Hampshire Fish and Game Department permit issued September 2, 2021).

Ethical statement

All work is original research carried out by the authors and has not been published elsewhere and is not being considered for publication elsewhere. All funding sources are acknowledged in the Acknowledgements section. All squirrel trapping and handling was conducted in accordance with our approved protocol from the University of Maine's Institutional Animal Care and Use Committee (IACUC A2018–11–02, A2021–12–01).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03539.

Data availability

Data and code are available on Figshare: https://figshare.com/articles/dataset/Data_Over_the_limit_Consequences_of_gray_squirrel_personality_on_the_shifting_range_limits_of_oak_and_hickory_species/27312384

References

Aubin, I., Garbe, C.M., Colombo, S., Drever, C.R., McKenney, D.W., Messier, C., Pedlar, J., Saner, M.A., Venier, L., Wellstead, A.M., Winder, R., Witten, E., Ste-Marie, C., 2011. Why we disagree about assisted migration: ethical implications of a key debate regarding the future of Canada's forests. For. Chron. 87 (6), 755–765. https://doi.org/10.5558/tfc2011-092.

Barnett, R.J., 1977. The effect of burial by squirrels on germination and survival of oak and hickory nuts. Am. Midl. Nat. 98 (2), 319–330. ⟨https://www.jstor.org/stable/2424983⟩.

Bates, D.M., Maechler, M., Bolker, B.M., & Walker, S. (2015). " Lme4: Linear Mixed-Effects Models Using Eigen and S4." ⟨https://cran.r-project.org/web/packages/lme4/lme4.pdf⟩.

Boone, S.R., Mortelliti, A., 2019. Small mammal tree seed selection in mixed forests of the Eastern United States. For. Ecol. Manag. 449, 117487. https://doi.org/10.1016/j.foreco.2019.117487.

Boone, S.R., Brehm, A.M., Mortelliti, A., 2021. Seed predation and dispersal by small mammals in a landscape of fear: effects of personality, predation risk and land-use change. Oikos 22 (2), 1–15. https://doi.org/10.1111/oik.08232.

Botanic Gardens Conservation International (BGCI) and IUCN (International Union for Conservation of Nature). 2018. *Carya cordiformis and Carya ovata. The IUCN Red List of Threatened Species.* ⟨https://www.iucnredlist.org⟩.

Box, G.E.P., Cox, D.R., 1964. An analysis of transformations. J. R. Stat. Soc. 26 (2), 211–243. https://doi.org/10.1111/j.2517-6161.1964.tb00553.x.

Boyer, N., Réale, D., Marmet, J., Pisanu, B., Chapuis, J.-L., 2010. Personality, space use and tick load in an introduced population of Siberian chipmunks *Tamias sibiricus*. J. Anim. Ecol. 79 3, 538–547. ⟨http://www.jstor.org/stable/40605424⟩.

Brehm, A.M., Mortelliti, A., 2022. Small mammal personalities generate context dependence in the seed dispersal mutualism. PNAS 119 (15), e2113870119. https://doi.org/10.1073/pnas.2113870119.

Brehm, A.M., Mortelliti, A., Maynard, G.A., Zydlewski, J., 2019. Land-use change and the ecological consequences of personality in small mammals. Ecol. Lett. 22 (9), 1387–1395. https://doi.org/10.1111/ele.13324.

Bubac, C.M., Miller, J.M., Coltman, D.W., 2020. The genetic basis of animal behavioural diversity in natural populations. Mol. Ecol. 29 (11), 1957–1971. https://doi.org/10.1111/mec.15461.

Carter, A.J., Marshall, H.H., Heinsohn, R., Cowlishaw, G., 2013. Personality predicts decision making only when information is unreliable. Anim. Behav. 86 (3), 633–639. https://doi.org/10.1016/j.anbehav.2013.07.009.

Case, S.B., Kawelo, K., Hoh, J., O'hearn, D., Sperry, J.H., Foster, J.T., Drake, D.R., Vizentin-Bugoni, J., Kelley, J.P., Tarwater, C.E., 2024. Effects of fruit novelty on feeding preference in four globally invasive frugivorous birds. Biol. Invasions. https://doi.org/10.1007/s10530-024-03436-w.

Cilles, S.E., Coy, G., Stieha, C.R., Cox, J.J., Crowley, P.H., Maehr, D.S., 2016. A comparison of seed predation, seed dispersal, and seedling herbivory in oak and hickory: Species with contrasting regenerating abilities in a bluegrass savanna-woodland habitat. Northeast. Nat. 23 (4), 466–481. https://doi.org/10.1656/045.023.0404.

David, M., Auclair, Y., Giraldeau, L.A., Cézilly, F., 2012. Personality and body condition have additive effects on motivation to feed in Zebra Finches *Taeniopygia guttata*. Ibis 154 (2), 372–378. https://doi.org/10.1111/j.1474-919X.2012.01216.x.

Davis, M.B., Shaw, R.G., 2001. Range shifts and adaptive responses to quaternary climate change. Sci 292 (5517), 673–679. https://doi.org/10.1126/science.292.5517.673.

Dingemanse, N.J., Wright, J., 2020. Criteria for acceptable studies of animal personality and behavioural syndromes. Ethol 126 (9), 865–869. https://doi.org/10.1111/eth.13082.

Fralish, J.S., 2004. The Keystone role of oak and hickory in the central hardwood forest. General Technical Report SRS-73. In: Spetich, M. (Ed.), In: *Upland oak ecology symposium: history, current conditions, and sustainability*. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, pp. 78–87. General Technical Report SRS-73.

Gómez, J.M., Schupp, E.W., Jordano, P., 2019. Synzoochory: the ecological and evolutionary relevance of a dual interaction. Biol. Rev. 94 (3), 874–902. https://doi.org/10.1111/brv.12481.

Gurnell, J., Lurz, P.W.W., Shuttleworth, C.M., 2016. Ecosystem impacts of an invader in Europe, the grey squirrel *Sciurus carolinensis*." In: *The grey squirrel: ecology & management of an invasive species in Europe*. In: Shuttleworth, C.M., Lurz, P.W.W., Gurnell, J. (Eds.), European Squirrel Initiative. Suffolk, Woodbridge, pp. 307–326.

Hadj-Chikh, L.Z., Steele, M.A., Smallwood, P.D., 1996. Caching behavior of gray squirrels: test of the perishability and handling-time hypotheses. Anim. Behav. 52 (5), 941–948. https://doi.org/10.1006/anbe.1996.0242.

Han, Q., Keeffe, G., 2021. Promoting climate-driven forest migration through large-scale urban afforestation. Lands Urb. Plan. 212, 104124. https://doi.org/10.1016/j.landurbplan.2021.104124.

Hopewell, L.J., Leaver, L.A., 2008. Evidence of social influences on cache-making by grey squirrels (*Sciurus carolinensis*). Ethol 114 (11), 1061–1068. https://doi.org/10.1111/j.1439-0310.2008.01554.x.

Humphreys, B.R., Mortelliti, A.M., 2024. Pilfering personalities: Effects of small mammal personality on cache pilferage (early view). J. Anim. Ecol.. https://doi.org/10.1111/1365-2656.14059.

Hunter, M.L., Boone, S.R., Brehm, A.M., Mortelliti, A., 2021. Modulation of ecosystem services by animal personalities. Front. Ecol. Environ. 20 (1), 58–63. https://doi.org/10.1002/fee.2418.

Hurley, J.C. 1989. "Importance and management of mast species other than oaks." In: *Proceedings of the Workshop: Southern Appalachian Mast Management*, McGee, C. E.(ed.). Knoxville, Tennessee, pp.74-82.

IPCC, 2022. In: Pörtner, H.-O., Roberts, D.C., Tignor, M., Poloczanska, E.S., Mintenbeck, K., Alegría, A., Craig, M., Langsdorf, S., Löschke, S., Möller, V., Okem, A., Rama, B. (Eds.), Climate Change 2022: Impacts, Adaptation and Vulnerability. Contributions of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge and New York, NY. https://doi.org/10.1017/9781009325844.

Koprowski, J.L., 1994. Sciurus carolinensis. Mamm. Species 2 (480), 1–9. https://doi.org/10.2307/3504224.

Koster, J., McElreath, R., 2017. Multinomial analysis of behavior: statistical methods. Behav. Ecol. Sociobiol. 71, 138. https://doi.org/10.1007/s00265-017-2363-8.

Lawlor, J.A., Comte, L., Grenouillet, G., Lenoir, J., Baecher, J.A., Bandara, R.M.W.J., Bertrand, R., Chen, I.-C., Diamond, S.E., Lancaster, L.T., Moore, N., Murienne, J., Oliviera, B.F., Pecl, G.T., Pinsky, M.L., Rolland, J., Rubenstein, M., Scheffers, B.R., Thompson, L.M., van Amerom, B., Villalobos, F., Weiskopf, S.R., Sunday, J., 2024. Mechanisms, detection and impacts of species redistributions under climate change. Nat. Rev. Earth Environ. 5, 351–368. https://doi.org/10.1038/s43017-024-00527-z.

Martin, J.G.A., Réale, D., 2008. Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. Anim. Behav. 75 (1), 309–318. https://doi.org/10.1016/j.anbehav.2007.05.026.

Martin, J.G.A., Nussey, D.H., Wilson, A.J., Réale, D., 2011. Measuring individual differences in reaction norms in field and experimental studies: a power analysis of random regression models: power analysis of random regression models. Methods Ecol. Evol. 2 (4), 362–374. https://doi.org/10.1111/j.2041-210x.2010.00084.x.

Mazzamuto, M.V., Cremonesi, G., Santicchia, F., Preatoni, D., Martinoli, A., Wauters, L.A., 2018. Rodents in the arena: a critical evaluation of methods measuring personality traits. Ethol. Ecol. Evol. 31 (1), 38–58. https://doi.org/10.1080/03949370.2018.1488768.

McElreath, R., 2020. Statistical Rethinking: A Bayesian Course with Examples in R and Stan (2nd edition. Chapman and Hall/CRC. https://doi.org/10.1201/9780429029608.

McKenney, D.W., Pedlar, J.H., Rood, R.B., Price, D., 2011. Revisiting projected shifts in the climate envelopes of North American trees using updated general circulation models. Glob. Chang. Biol. 17 (8), 2720–2730. https://doi.org/10.1111/j.1365-2486.2011.02413.x.

Merz, M.R., Boone, S.R., Mortelliti, A., 2023. Predation risk and personality influence seed predation and dispersal by a scatter-hoarding small mammal. Ecosphere 14 (1), e4377. https://doi.org/10.1002/ecs2.4377.

Mortelliti, A., 2023. The importance of animal behavior for ecosystem services. TREE 38 (4), 320–323. https://doi.org/10.1016/j.tree.2022.10.009.

Mortelliti, A., Brehm, A.M., 2020. Environmental heterogeneity and population density affect the functional diversity of personality traits in small mammal populations. Proc. R. Soc. B. 287, 20201713. https://doi.org/10.1098/rspb.2020.1713.

Mortelliti, A., Grentzmann, I.P., Fraver, S., Brehm, A.M., Calkins, S., Fisichelli, N., 2019. Small mammal controls on the climate-driven range shifts of woody plant species. Oikos 128 (12), 1726–1738. https://doi.org/10.1111/oik.06643.

Muñoz, A., Bonal, R., 2008. Are you strong enough to carry that seed? Seed size/body size ratios influence seed choices by rodents. Anim. Behav. 76 (3), 709–715. https://doi.org/10.1016/j.anbehav.2008.03.017.

Neuschulz, E.L., Mueller, T., Schleuning, M., Böhning-Gaese, K., 2016. Pollination and seed dispersal are the most threatened processes of plant regeneration. Sci. Rep. 6, 29839. https://doi.org/10.1038/srep29839.

Park, A., Talbot, C., 2012. Assisted migration: uncertainty, risk and opportunity. For. Chron. 88 (4), 412–419. https://doi.org/10.5558/tfc2012-077.

Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42. https://doi.org/10.1038/nature01286.

Peters, M.P., Prasad, A.M., Matthews, S.N., Iverson, L.R., 2020. Climate change tree atlas, Version 4. U.S. Forest Service. Northern Research Station and Northern Institute of Applied Climate Science, Delaware, OH. ⟨https://www.nrs.fs.fed.us/atlas⟩.

Réale, D., Dingemanse, N.J., Kazem, A.J.N., Wright, J., 2010. Evolutionary and ecological approaches to the study of personality. Philos. Trans. R. Soc. B-Biol. Sci. 365 (1560), 3937–3946. https://doi.org/10.1098/rstb.2010.0222.

Santicchia, F., Wauters, L.A., Dantzer, B., Westrick, S.E., Ferrari, N., Romeo, C., Palme, R., Preatoni, D.G., Martinoli, A., 2020. Relationships between personality traits and the physiological stress response in a wild mammal. Curr. Zool. 66 (2), 197–204. https://doi.org/10.1093/cz/zoz040.

Sih, A., Bell, A., Johnson, J.C., 2004. Behavioral syndromes: An ecological and evolutionary overview. TREE 19 (7), 372–378. https://doi.org/10.1016/j.tree.2004.04.009.

Sittaro, F., Paquette, A., Messier, C., Nock, C.A., 2017. Tree range expansion in eastern North America fails to keep pace with climate warming at northern range limits. Glob. Chang. Biol. 23 (8), 3292–3301. https://doi.org/10.1111/gcb.13622.

Smith, B.R., Blumstein, D.T., 2013. Animal personality and conservation biology: the importance of behavioral diversity. In: Carere, C., Maestripieri, D. (Eds.), In: *Animal Personalities: Behavior, physiology, and evolution*. The University of Chicago Press, Chicago and London, pp. 381–413. https://doi.org/10.7208/9780226922065-015.

Stan Development Team. 2024. “RStan: the R interface to Stan.” version 2.32.6, ⟨https://mc-stan.org/⟩.

Steele, M.A., 2021. Oak Seed Dispersal: A Study in Plant-Animal Interactions. Johns Hopkins University Press, Baltimore, Maryland.

Steele, M.A., Yi, X., 2020. Squirrel-seed interactions: the evolutionary strategies and impact of squirrels as both seed predators and seed dispersers. Front. Ecol. Evol. 8, 259. https://doi.org/10.3389/fevo.2020.00259.

Steele, M.A., Manierre, S., Genna, T., Contreras, T.A., Smallwood, P.D., Pereira, M.E., 2006. The innate basis of food-hoarding decisions in gray squirresls: evidence for behavioural adaptations to the oaks. Anim. Behav. 71 (1), 155–160. https://doi.org/10.1016/j.anbehav.2005.05.005.

Steele, M.A., Halkin, S.L., Smallwood, P.D., McKenna, T.J., Mitsopoulos, K., Beam, M., 2008. Cache protection strategies of a scatter-hoarding rodent: do tree squirrels engage in behavioural deception? Anim. Behav. 75 (2), 705–714. https://doi.org/10.1016/j.anbehav.2007.07.026.

Thompson, D.C., 1978. The social system of the grey squirrel. Behav 64 (3), 305–328. ⟨https://www.jstor.org/stable/4533876⟩.

Tourville, J., Dovciak, M., 2023. Small mammal granivory as a biotic filter for tree establishment beyond elevation range boundaries. Plant Ecol. 224, 435–447. https://doi.org/10.1007/s11258-023-01305-5.

Tranquillo, C., Santicchia, F., Romeo, C., Bisi, F., Panzeri, M., Preatoni, D., Martinoli, A., Alberdi, A., Wauters, L.A., 2024. Going urban: variation in personality traits of an invasive species along an urbanization gradient. *gyae077* J. Mammal.. https://doi.org/10.1093/jmammal/gyae077.

USGS (U.S. Geological Survey). 1999. From “Digital representation ‘Atlas of United States Trees’ by Elbert L. Little, Jr.” ⟨https://web.archive.org/web/20170127093428/https://gec.cr.usgs.gov/data/little/⟩.

Vander Wall, S.B., 2000. The influence of environmental conditions on cache recovery and cache pilferage by yellow pine chipmunks (*Tamias amoenus*) and deer mice (*Peromyscus maniculatus*). Behav. Ecol. 11 (5), 544–549. https://doi.org/10.1093/beheco/11.5.544.

Wang, B., Ye, C.X., Cannon, C.H., Chen, J., 2013. Dissecting the decision making process of scatter-hoarding rodents. Oikos 122 (7), 1027–1034. ⟨https://www.jstor.org/stable/41937755⟩.

Wauters, L.A., Tosi, G., Gurnell, J., 2002. Interspecific competition in tree squirrels: do introduced grey squirrels (*Sciurus carolinensis*) deplete tree seeds hoarded by red squirrels (*S. vulgaris*)? Behav. Ecol. Sociobiol. 51, 360–367. https://doi.org/10.1007/s00265-001-0446-y.

Wauters, L.A., Tosi, G., Gurnell, J., 2005. A review of the competitive effects of alien grey squirrels on behavior, activity, and habitat use of red squirrels in mixed, deciduous woodland in Italy. *Hystrix It.* J. Mamm. 16 (1), 27–40. ⟨http://www.italian-journal-of-mammalogy.it/pdf-77444-13646?filename= 13646.pdf⟩.

Wauters, L.A., Lurz, P.W.W., Santicchia, F., Romeo, C., Ferrari, N., Martinol, A., Gurnell, J., 2023. Interactions between native and invasive species: a systematic review of the red squirrel-gray squirrel paradigm. Front. Ecol. Ecol. 11, 2023. https://doi.org/10.3389/fevo.2023.1083008.

Xiao, Z., Jansen, P.A., Zhang, Z., 2006. Using seed-tagging methods for assessing post-dispersal seed fate in rodent-dispersed trees. For. Ecol. Manag. 223 (1-3), 18–23. https://doi.org/10.1016/j.foreco.2005.10.054.

Zhu, K., Woodall, C.W., Clark, J.S., 2012. Failure to migrate: lack of tree range expansion in response to climate change. Glob. Chang. Biol. 18 (3), 1042–1052. https://doi.org/10.1111/j.1365-2486.2011.02571.x.

Zwolak, R., Sih, A., 2020. Animal personalities and seed dispersal: a conceptual review. Funct. Ecol. 34 (7), 1294–1310. https://doi.org/10.1111/1365-2435.13583.