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ARTICLE
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Multi-cohort survival of northern red oak seedlings at a northern hardwood forest transition

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Abstract

Global change has created less stable forest systems and given urgency to understanding limitations to the establishment of tree seedlings beyond current range boundaries. We quantified trends in 13 years of annual northern red oak (QURU) seedling survival data for 1733 marked individuals at a local species distribution boundary within the northern hardwood forest in New Hampshire, USA. Over the study period, the median distance of seedlings into the valley did not change, although there was a net gain of 89 plots (5 m^2) occupied. For a subset of seedlings that were marked in their year of birth ($N = 937$), we examined relationships among terrain, vegetation community, and initial individual seedling traits, and evaluated their effects on time to seedling mortality using a parametric accelerated failure time model. The year of seedling germination had the largest effect on survival with increasing mortality rates for seedlings from more recent cohorts. Seedlings had longer survival times where oak seedling densities were lower, shrub cover was higher, and when the acorn remained attached. Additionally, survival time was increased in higher elevation plots, which were also located further into the valley. Interannual seedling survival ($N = 1580$) was strongly impacted by seedling condition in the previous year, particularly leaf number and amount of leaf damage. Most seedling deaths occurred over winter, and seedlings failed to break bud the following spring. Interannual variation in seasonal climate, particularly deep, heavy snowpack in 2019 followed by drought conditions in 2020, coincided with recent elevated mortality. Overall, the median survival time of 3–4 years and the rapid turnover of the oak seedling population currently limit ability for expansion, although the net gain of occupied plots and increase in survival at higher elevation plots with lower QURU densities present some mechanisms that could promote expansion if the current suboptimal understory conditions shift to favor QURU.

KEYWORDS
Hubbard Brook Experimental Forest, local range edge, mortality, *Quercus rubra* L., seedling environment, seedling traits

INTRODUCTION

Tree species distributions are becoming more uncertain in the face of novel, interacting stressors including climate change, introduced pests and pathogens, and altered disturbance regimes (Rogers et al., 2017; Woodall et al., 2018). Recent evidence suggests tree species may not have the ability to keep pace with global change (Etterson et al., 2020; Sittaro et al., 2017). Reasons for this lag include edaphic restrictions (Brown & Vellend, 2014) and priority effects imposed by current forest species (Boisvert-Marsh & de Blois, 2021; Clark et al., 2022; Sparbanie & Snell, 2022). Predicting shifts in tree species distributions requires a deeper understanding of limitations to tree establishment (Boisvert-Marsh & de Blois, 2021; Sparbanie & Snell, 2022). Long-term empirical evidence of seedling dynamics at current range edges can help fill the knowledge gap regarding the patterns and processes of tree species migration in the era of global change.

Northern (poleward) range limits are most often thought to be determined by cold temperatures, and are therefore expected to respond to climate warming (Jones & Gilbert, 2016). The northern red oak (*Quercus rubra* L.; hereafter QURU) is one such tree species expected to expand its range poleward into northern New England in response to a warming climate (Iverson, Peters, et al., 2019). QURU is an ecologically and economically important tree species that occurs farther North than any other North American oak (Burns & Honkala, 1990). However, QURU altitudinal distributions in the region have remained unchanged for the past 8000 years based on palynological evidence (Spear et al., 1994). Cogbill et al. (2002) described the New England tension zone where both pre- and post-settlement forests in New England shift from QURU-dominated (Southeast) to beech-dominated (Northwest). This tension zone matches closely with mean annual temperatures greater than 8°C (Cogbill et al., 2002) suggesting an important role of climate in stabilizing the current QURU distribution.

In addition, regeneration failure of QURU is common throughout its range with suspected causes including seed predation, herbivory, pathogens, late frost damage, limited dispersal, insufficient light at the forest floor, and competition (Iverson et al., 2008; Knott et al., 2019). These limitations could inhibit the projected northward range expansion of QURU even as warming expands suitable habitat (Mohan et al., 2009). Paradoxically, QURU has performed better than other tree species tested in recent population expansion experiments where it has been planted outside current local distribution limits (Clark et al., 2022) suggesting that the climate may have already shifted sufficiently to favor QURU seedling survival. However, regional-scale shifts in tree distribution will need to overcome the potential demographic bottlenecks of dispersal and establishment.

In QURU stands, terrain features have often been linked to higher abundance of QURU regeneration, particularly aspect (Fei & Steiner, 2008; Johnson et al., 2019; Kabrick et al., 2014), although the relationships are not consistent between studies likely due to the context-dependent relationships between QURU and terrain. In some parts of the distribution, QURU might need south or southwest facing slopes, while in other areas it occurs at higher elevations on ridge tops (Collins & Carson, 2004). For the northern hardwood forest, Bormann et al. (1970) documented the importance of the complex elevation gradient in shaping tree species composition. Thus, there is good evidence to suggest that terrain features like slope, aspect, and elevation would influence QURU range expansion, but the specific effects have not been examined for our study area.

For a seedling expanding into a new climate-suitable habitat, the absence of conspecific adults could improve establishment success by avoiding enemies (i.e., Janzen-Connell negative density dependence; Jevon et al., 2022) or decrease success if parents facilitate establishment such as through mycorrhizal networks (Jones & Gilbert, 2016). For QURU, one of the biggest vulnerabilities to migration was pest and pathogen effects (Rogers et al., 2017). In addition, Jevon et al. (2022) found QURU seedlings grew taller and survived better under pines compared with conspecifics. In a longer-term forestry manipulation, both natural and planted QURU regenerated better in pine-dominated stands (Granger et al., 2018) and the same pattern has been found in Europe where QURU is naturalizing (Dyderski et al., 2020). Therefore, stand composition, particularly distance from adult QURU influence, high conspecific seedling densities, and the amount of conifer dominance may be important factors in QURU establishment.

In addition to the terrain and the forest community, individual seedling traits are important immediate determinants of seedling survival. For example, acorn size is a key trait with larger acorns producing larger seedlings

(Jevon et al., 2021; Popovic et al., 2015; Ramirez-Valiente et al., 2009) that are more likely to survive (Badano & Sanchez-Montes de Oca, 2022; Johnson et al., 2019). Large-seeded species such as QURU tend to have first-year seedlings that are comparatively insensitive to changes in abiotic factors as they have more initial resources from the seed (García & Houle, 2005). However, by the second year this benefit wanes and light availability becomes a critical determinant of QURU seedling survival (Brose, 2011; Canham et al., 1996).

The year of germination can lead to differences in seedling survival based on interannual differences in many factors and their interactions that are known to impact seedling survival such as seed production and predation (Janzen, 1971), initial seedling densities (Hett, 1971), annual climate (Dyderski & Jagodziński, 2019), and prevalence of damage agents (Gardescu, 2003). Interannual variation in seed production and initial seedling densities may be particularly relevant for masting species such as QURU. Interannual variation in climate or seedling damage agents may also lead to years with higher mortality regardless of seedling age. Careful documentation of annual differences is necessary to pinpoint causes of mortality (e.g., Dyderski & Jagodziński, 2019; Gardescu, 2003).

Here, we used a long-term (13 years) study of QURU at a range edge to document patterns of QURU expansion into the northern hardwood forest, and to quantify the determinants of seedling survival at the population and individual seedling scale. Importantly, our forest study encompasses variation in terrain features and forest composition at this range edge. For example, QURU seedlings span an elevation range from 245 to 470 m and a composition gradient from conifer dominance to hardwood dominance. Information from our repeat inventories allowed us to not only identify the traits linked to seedling survival but also evaluate the variation associated with annual seedling cohorts (Johnson et al., 2019).

Given the host of potential influences on QURU establishment, we organized drivers of population survival into four categories: terrain features, community properties, individual traits, and cohort effects. For individual seedling survival, we formally considered previous season condition metrics and retrospectively variation in annual climate and biotic damage agents, which could not be accommodated in the population model. Therefore, the population model captures the possible spatial effects (terrain and community) and initial seedling condition effects, while the individual survival considers temporal (interannual) variation effects. Our overall objectives were to: (1) document the pattern of oak seedling occurrence in our study site and any changes in occurrence over the 13-year period; and (2) explore factors determining red oak seedling survival at the population (spatial) and individual (temporal) scales. We posed two non-exclusive hypotheses for oak seedling expansion in the study area: (1) lower seedling densities further in the valley contributed to higher seedling survival for the more recent cohorts; (2) more favorable climatic conditions and/or lower levels of leaf damage increased seedling establishment success. Alternatively, the lack of expansion could be explained by three non-exclusive factors: (1) lower seedling survival at higher elevation plots; (2) uniformly low seedling survival with populations maintained mainly by input of new acorns; and (3) unfavorable pest or climate conditions that persisted throughout the study period.

METHODS

Study site

The Hubbard Brook Experimental Forest (HBEF) is a Long-Term Ecological Research (LTER) site with an area of 3160 ha located in the White Mountain National Forest in central New Hampshire (43°56′ N, 71°45′ W) (Figure 1). The terrain is a bowl-shaped valley with Hubbard Brook running along the bottom. HBEF is primarily a northern hardwood forest, composed of a mixture of *Acer saccharum* Marsh (sugar maple), *Fagus grandifolia* Ehrh. (American beech), and *Betula alleghaniensis* Britt. (yellow birch). At lower elevations in the valley there are dense stands dominated by *Tsuga canadensis* (L.) Carr. (Eastern hemlock) (van Doorn et al., 2011). Soils are primarily well-drained, acidic spodosols formed from glacial till of varying thicknesses (Bailey et al., 2014). Plots for this study occur in the lower Eastern half of the valley (245–470 m above sea level [asl] elevation) and were centered on long-term tree plots termed "valleywide" (van Doorn et al., 2011; Figure 1; Table 1).

The HBEF sits at the northern edge of the QURU range and provides a study site where seedlings persist without the presence of parent trees (Peters et al., 2020). Climatic conditions include long cold winters and short, cool summers. Mean January and July temperatures are −8 and 19°C, respectively (USDA, 2022a). The mean annual temperature at the headquarters station closest to the Eastern entrance is 6.3°C; however, temperatures have been increasing at HBEF (USDA, 2022a), and for the first time in the 68-year record, three of the study years (2016, 2021, and 2022) had mean annual temperature >8°C: a critical threshold for QURU distribution (Cogbill et al., 2002). HBEF has an average annual precipitation of 1300 mm, about one third of which falls as snow (Bailey et al., 2003; USDA, 2022b). A snowpack is typically present from December to mid-April.

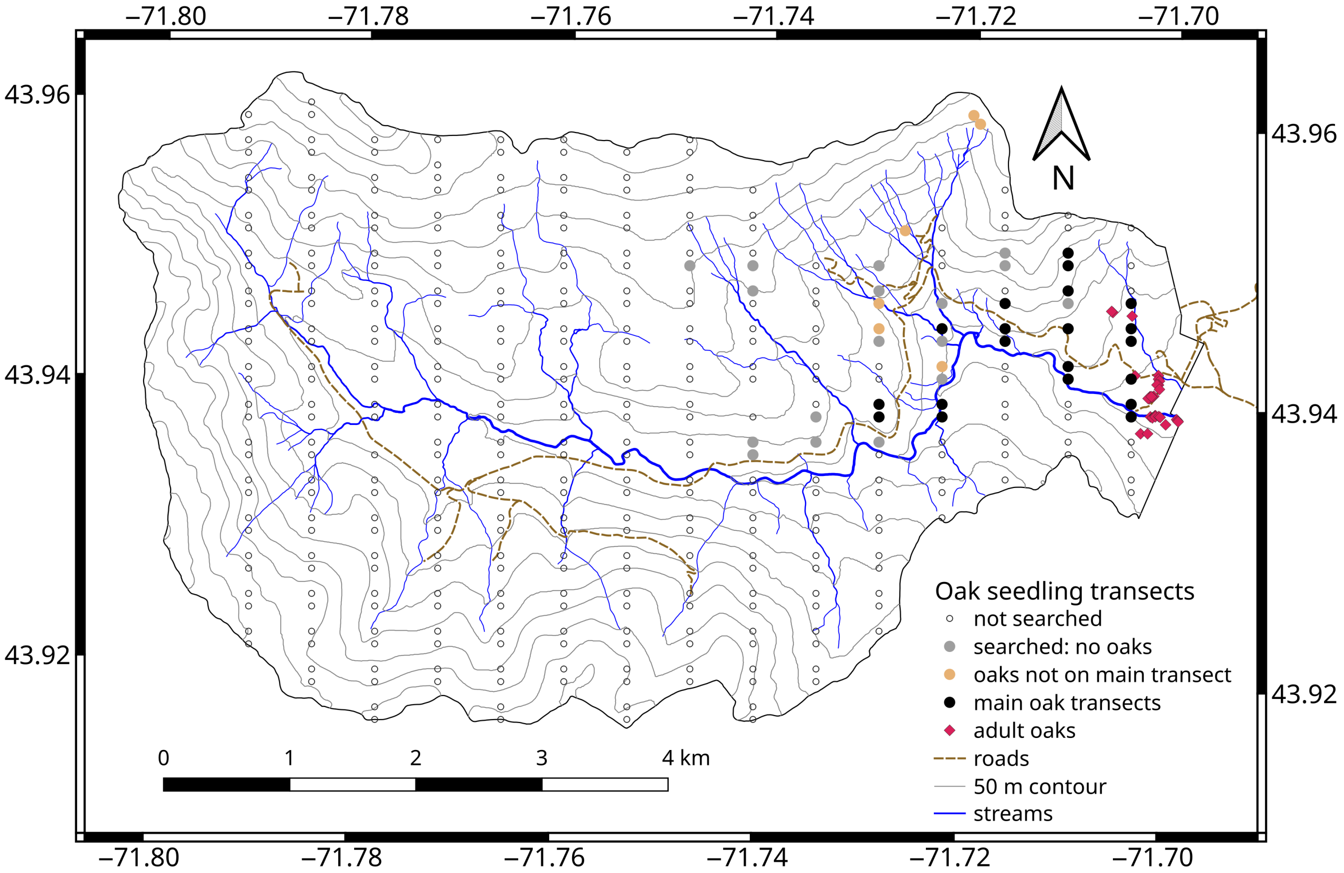

FIGURE 1 Map of northern red oak seeding surveys in the Hubbard Brook Experimental Forest, NH. The dots represent the location of the valleywide plots that serve as the center point for oak seedling searches and mapping. The red diamonds denote adult oak trees ($N = 31$) mapped in the forest. Contour lines are 50 m contours.

Seedling surveys

In 2011, 40 long-term plots at HBEF were searched for the presence of QURU seedlings, and 23 of these transects had individual QURU seedlings present that were marked within a 2000-m^2 search area (80 possible 25 m^2 plots; Figure 1; Appendix S1: Figure S1). In 2013, a 24th transect was added when an oak seedling was found there. The search areas were delineated as a belt-transect running 100 m east and west of the plot center and 5 m to the north and south of the center line. This area was searched by at least two people by walking slowly along one side of the center line with one person searching the inner 2.5 m area and the second person scanning the outer 2.5 m area. All QURU seedlings (<1.5 m in height) were given a unique number and mapped with distance and direction in reference to the center transect line (Appendix S1: Figure S1). Seedlings were then measured for vertical height from the ground, number of leaves, age, and presence of an attached acorn if two years old or younger. Seedlings were aged by counting back bud scars from the terminal bud. From 2012 to 2023, all marked individuals were assessed for survival, vertical height, and leaf number. The transects were surveyed in the same manner in most years in late summer and new recruits were marked, mapped, and measured in the same manner. In 2012 and 2020, all marked seedlings were assessed but the full 2000-m^2 area was not searched for new seedlings due to known low seedling input and lack of personnel and time.

Starting in 2015, live seedlings were also inspected for leaf damage, measured on a five-point scale (less than 5% damage, 6%–25% damage, 26%–50% damage, 51%–75% damage, and greater than 75% damage), and branch dieback, measured as the ratio of live branches to total branches (i.e., live and dead). Based on the patterns of damage, some agents of damage were distinguished, specifically spider webs, caterpillar herbivory, other insect herbivory, mammal browse, rodent clipping, and fungal damage. Other causes of damage included flooding, litter burial, and stem breaking. Dead seedlings were classified for death agents in the field or retrospectively (seedlings previously noted as severely damaged by particular agents). Many dead seedlings had failed to break bud and were regarded as dying over winter unless severe damage had been noted the previous year.

TABLE 1 Description of landscape position for 20 study transects with marked northern red oak seedlings in Hubbard Brook Experimental Forest, NH.

Transect	Distance into valley (m)	Elevation (m asl)	Slope[a] (%)	Aspect range (°)
396	437–632	270	26 (53)	10–205
354	452–642	245	7 (33)	50–341
353	565–707	250	8 (19)	166–205
352	757–880	320	18 (35)	74–252
351	840–956	330	21 (41)	39–222
337	989–1080	310	19 (41)	117–223
350	1017–1114	350	23 (78)	43–237
338	1026–1155	330	7 (22)	76–198
339	1180–1336	330	11 (33)	81–260
341	1387–1489	400	22 (33)	100–135
342	1549–1656	435	24 (33)	59–131
335	1611–1760	350	12 (38)	95–228
343	1617–1728	460	23 (38)	102–186
336	1624–1736	340	15 (37)	156–212
334	1769–1850	410	17 (41)	160–271
379	1952–1967	370	20 (52)	13–329
378	1985–2130	370	30 (71)	14–335
322	2070–2235	368	26 (44)	60–209
317	2437–2572	465	16 (51)	82–250
316	2564–2579	470	24 (40)	30–259

Abbreviation: asl, above sea level.

[a] For slope, the mean is given with maximum value for the transect in parentheses.

In 2019 and 2020, plant community covariables were measured by dividing the study transects into 80 contiguous plots that were 25 m^2 in area. For all such plots containing at least one marked QURU seedling, data were collected at the center of these plots ($N = 381$ plots with full environmental data) (Appendix S1: Figure S1). Therefore, the number of plots sampled per transect varied (Table 2). Tree composition was recorded, and basal area was measured with a prism sweep (2.5 factor metric basal area) from plot center; shrub cover in the plot was estimated visually by consensus. We quantified understory light availability, slope percent, and aspect along the transects (transect center, 10, 30, 50, 70, and 90 m east and west of center; Appendix S1: Figure S1). For analysis, aspect was transformed using the Beers' equation (Beers et al., 1966) that produces unitless values that range from 2 (45°; least solar input) to 0 (225°; most solar input).

Understory light availability was characterized at each 20-m interval point with hemispherical photographs ($N = 11$ photographs per transect area). All photos were taken at 1 m height under diffuse light conditions using a scientific grade photographic lens (Nikon 8 mm) and a digital single-lens reflex camera (Nikon digital Df). Understory foliage or branches within 0.5 m of the lens were moved out of the viewshed to insure a clear photo. Distortions in the area projections (Herbert, 1987) were corrected prior to analysis. We used the Gap Light Analyzer software to compute the fraction of total transmitted radiation reaching each photo point during the growing season (Canham, 1988; Frazer et al., 1999). The above-canopy radiation model was based on long-term results from the headquarters weather station at HBEF (USDA, 2019). Light levels were reported as the percent of above-canopy total transmitted radiation (% TT) received during the growing season (May 15–August 31). Precision error associated with photographic analyses was 7.6% of relative root mean squared error (rRMSE). For the low light conditions in these forests, this error represents ±0.44 percentage unit precision of % TT.

Distance into the valley (in meters) and elevation (in meters above sea level) were also included for each 25 m^2 plot containing a seedling for a total of 569 plots over the study period. We created a dataset with the total number of QURU seedlings in the plot, number of new seedlings establishing into the plot after initial 2011 survey, and number of years with at least one QURU seedling in the plot. We used this data set to examine the pattern of plot occupancy in the valley and over time.

Data analysis

Overview

As noted above, we organized the potential determinants of QURU survival into four categories: cohort effects, terrain features, community properties, and individual seedling traits. To evaluate patterns in environmental characteristics and QURU seedling distribution, we used basic parametric statistics (e.g., curve fitting, analysis of variance, and χ^2 tests). These tests were conducted using JMP 14.0 (SAS Institute, Cary, NC). Annual seedling mortality was expressed as a discrete rate variable (Sheil et al., 1995). We estimated uncertainty in annual mortality by simulating 1000 random samples from a binomial distribution defined by the sample sizes and probabilities calculated for each year.

To test our ideas about the relative importance of these determinants on QURU recruitment, we used failure time analysis to estimate the effect of these metrics on the survivorship of QURU seedlings. Our field measurements produced a total of 13 metrics with at least

TABLE 2 Plant community covariables for 381 25 m^2 plots with marked northern red oak seedlings nested in 20 study transects in Hubbard Brook Experimental Forest, NH.

Transect	**25 m^2 plots with oaks[a] (%)**	**Oak seedlings[b] in 25 m^2**	**Hemlock[c] (%)**	**Transmitted light[c] (%)**	**Tree basal area[b] (m^2 ha^{-1})**	**Shrub cover[b] (%)**
396	72.5	4.4 (0.6)	53.2 (100)	6.8 (10.4)	30.0 (1.2)	15.0 (2.4)
354	73.7	4.4 (0.5)	52.6 (85.7)	8.8 (11.6)	32.5 (1.2)	14.9 (3.5)
353	78.7	5.2 (0.5)	39.4 (71.4)	10.3 (13.4)	37.5 (1.2)	8.9 (1.6)
352	68.8	3.7 (0.4)	40.3 (75.0)	8.3 (11.5)	27.5 (1.2)	17.8 (4.3)
351	71.3	3.0 (0.3)	39.1 (80.0)	6.0 (8.6)	25.0 (1.2)	17.5 (2.8)
337	22.5	1.5 (0.2)	41.0 (83.3)	7.2 (10.0)	27.5 (2.0)	3.9 (1.5)
350	70.0	2.1 (0.3)	21.4 (47.1)	9.1 (13.8)	30.0 (1.5)	11.4 (2.1)
338	38.8	2.3 (0.3)	33.2 (71.4)	5.3 (7.2)	30.0 (1.0)	11.5 (3.3)
339	33.8	2.2 (0.3)	10.2 (30.8)	7.3 (11.4)	32.5 (1.2)	19.0 (5.2)
341	18.8	2.0 (0.4)	0.0 (0)	5.5 (6.8)	42.5 (2.5)	20.0 (6.4)
342	22.5	1.7 (0.2)	0.0 (0)	3.6 (4.9)	32.5 (2.0)	7.5 (2.1)
335	22.5	1.3 (0.2)	0.0 (0)	5.2 (8.9)	35.0 (1.2)	9.7 (2.6)
343	21.3	1.4 (0.3)	0.0 (0)	2.4 (4.6)	30.0 (2.5)	6.1 (2.2)
336	15.0	1.8 (0.6)	0.0 (0)	6.1 (7.5)	30.0 (2.0)	5.4 (1.8)
334	5.0	1.0 (0)	2.4 (7.1)	3.7 (4.7)	25.0 (2.2)	27.0 (4.7)
379	3.8	1.0 (0)	39.9 (42.9)	5.9 (6.0)	32.5 (0.3)	10.0 (10)
378	6.3	1.7 (0.7)	28.6 (66.7)	6.0 (6.5)	37.5 (0.8)	21.7 (9.4)
322	15.0	1.3 (0.1)	52.9 (81.8)	6.2 (8.9)	30.0 (1.8)	21.3 (9.5)
317	2.5	1.5 (0.5)	22.2 (33.3)	7.4 (8.7)	20.0 (3.8)	43.5 (6.5)
316	5.0	1.3 (0.3)	12.6 (20)	7.0 (8.0)	35.0 (5.2)	11.0 (7.4)

[a] Percent of the 80 possible 25 m^2 plots per transect.

[b] For seedling density, tree basal area, and shrub cover, the mean is given with the standard error for the transect in parentheses.

[c] For percent hemlock and transmitted light, the mean is given with maximum value for the transect in parentheses.

one metric in each category (Appendix S2: Table S1). We followed this population-level survival analysis with a detailed seedling-level analysis of plant traits and ecological agents that influence the probability of annual survival. Specifically, we used logistic regressions to quantify the year-to-year variation in seedling survival. Together these two analytical frameworks provide a comprehensive perspective of the establishment dynamics of QURU range expansion.

Failure time analysis

We evaluated the relative importance of 13 potential determinants of QURU seedling survival using an accelerated failure time (AFT) model. Conceptually, AFT is a parametric model that defines a baseline survival curve that can include covariates that speed up or slow down the survival times of individuals (James, 2014). Initial inspection of the baseline survival curve using the Kaplan–Meier estimator, a nonparametric technique for estimating and visualizing survival probability over time (Kaplan & Meier, 1958), suggested that an exponential distribution was the most appropriate parametric distribution for our AFT analysis (Appendix S1: Figure S2). We implemented our AFT analysis in R (R Core Team, 2021) with an exponential distribution and assigned the 13 potential determinants as covariables. All covariables were centered and scaled (mean = 0, SD = 1) prior to model estimation to facilitate robust estimation and intercomparison of parameters. We used the package *flexsurv* (https://cran.r-project.org/web/packages/flexsurv/flexsurv.pdf) to fit our models.

We applied an information theoretic approach to select the best AFT model (Burnham & Anderson, 2002). Our model selection procedure followed a three-step process. The first step was to screen for covariable importance by comparing the performance of all single-covariable AFT models to the null model (i.e., survival model with no covariables). The criterion for inclusion relied on the difference in Akaike information criterion (ΔAIC) between the null model and the single covariable models. If the AIC of the single covariable model was at least two units smaller than the null model (Burnham & Anderson, 2002), it was included for further consideration. The second step was to develop model selection "guideposts." These guideposts included the null model, a full model (all covariables that passed the initial screening), a model with all the terrain covariables, a model with all the community covariables, a model with all the plant covariables, and the model with the cohort covariable. We also calculated a covariance matrix for the covariables and flagged the pairs with high correlation. The third step used these guideposts and the covariation matrix to develop a candidate set of final models. The final model with the lowest AIC score was considered the best model. To check for lack of fit, we compared the survivorship curve of our best AFT model with the Kaplan–Meier survivorship curve.

In the population survival analysis, we only included seedlings that were marked and measured in the year they germinated and that occurred in the 381 25 m^2 plots with complete environmental measures ($N = 937$). For effect size comparisons, we used the exponential formula to transform the estimated covariable coefficients in the best model so that they could be interpreted as a multiplicative shortening (i.e., accelerated failure) or lengthening (i.e., decelerate failure) of the seedling lifetime relative to baseline survival.

Given the potential importance of seedling size differences in interpreting cohort differences, seedling initial height, initial leaf number and presence/absence of their acorn, were compared using the same subset ($N = 937$) of seedlings that were used in the population survival analysis. For comparisons of seedling traits between cohorts we used nonparametric comparisons because of the naturally unequal sample sizes. Continuous variables (height and leaf number) were compared with nonparametric ANOVA (Kruskal–Wallis) and posthoc tests with year as the factor. Categorical (presence/absence) acorn data were compared with contingency analysis by year in JMP 14.0 (SAS Institute).

Logistic regression analysis

We examined the relationship between seedling condition and whether they lived or died in the following season for all seedlings ($N = 1733$). Seedling condition in the previous season was assessed by several possible metrics: change in height (in centimeters) calculated as (height in season_{x-1}) − (height in season_{x-2}), seedling vertical height (in centimeters), leaf number, percent of branches that were alive (live branches/total branches × 100) and leaf damage (categorical, 0–4 scale, with 4 being more than 76% of leaf area damaged, see seedling measures for full details). Rather than testing for differences between measures for live and dead seedlings, we tested how well each metric fit the logistic regression for seedling death. Because of high correlation between these variables, we examined all possible univariate models to select the condition metrics that best fit seedling death patterns based on deviance reduction. We then summarized the impact of the odds ratios for these metrics. Logistic regression models were fitted using JMP 14.0 (SAS Institute).

RESULTS

Spatial environment and pattern of QURU occurrence

For adult occurrence, we found and mapped 31 canopy QURU in the eastern end of the valley with the furthest QURU at 1200 m into the valley (Figure 1). For seedling occurrence, we searched 41 valleywide areas and found QURU seedlings in 24 of these transects with seedling presence dropping to indetectable past 2.5 km into the valley (Figure 1). The main 20 study transects encompassed a full range of topographic positions in the lower valley (Table 1; Figure 1). Hemlock dominance ranged from absent (5 transects) to dominant (greater than 50% of trees; 3 transects) (Table 2). Tree basal area around the plots ranged from 18.8 to 43.5 m^2 ha^{-1} (Table 2). Light transmission was uniformly low (<10%) and was lowest in the hardwood-dominated plots (Table 2; Appendix S2: Table S2). Distance into the valley was related to several environmental variables. Light transmission and hemlock dominance decreased with distance further West into the valley, while elevation and plot steepness increased (Appendix S2: Table S2). Shrub cover varied from 3.9% to 43.4% with no pattern related to distance into the valley (Table 2; Appendix S2: Table S2).

During the course of the study, our dataset included 1733 marked individual QURU seedlings in 569 5 m^2 plots over the 24 transects (Table 2; for 20 main transects). Overall, QURU seedlings occurred in a third of the searched plots. Most plots had only one seedling (41%; 232 plots) and only 4% (26 plots) of the plots had 10 or more seedlings, with a maximum occupancy of 3.8 seedlings m^{-2} in one plot. Seedling occupancy (number of seedlings occurring in plots over 13 years) and the number of seedling establishment events (number of times new seedlings were marked in the plot) both decreased exponentially with distance into the valley (Appendix S1: Figure S3). Plots were evenly divided between having a single establishment event ($N = 286$) or more than one establishment event ($N = 283$). Plots with more than one establishment event had a median distance of 800 m into the valley with a maximum distance of 1742 m (Appendix S1: Figure S4). The number of plots with marked seedlings has varied during the study period. Currently there are 89 more plots occupied than at study initiation with the greatest gain in 2015 (gain of 105 plots) and the greatest loss in 2020 (62 plots) (Figure 2). Plots with seedlings newly marked throughout the study ($N = 374$) versus initial plots (2011; $N = 195$) were further into the valley (119 m; $\chi^2 = 11.69$; df = 1; $p = 0.0006$) and higher elevation (19.3 m asl.; $\chi^2 = 9.59$; df = 1; $p = 0.002$). The median distance of QURU seedlings into the valley has not increased over the course of the study and remains centered around 800 m from the East entrance as the bulk of seedlings are still at lower elevation closer to the valley entrance (Figure 2).

Cohort years 2011, 2015, and 2017 had a greater influx of seedlings (>100) whereas 2018 and 2022 had intermediate input (50–100) and other years post 2011 had less than 50 seedlings (Figure 3). In four years (2011, 2015, 2017, and 2022) with many new seedlings marked, seedlings were noted if they occurred in clumps (likely due to rodent caches). The number of seedlings in clumps ranged from 8.4% to 17.2% with an average of 10%.

Population survival analysis

Based on our initial screening, seven of the single-covariable AFT models provided more information than the null model (Appendix S2: Table S1). The best model excluded two highly correlated covariables (distance into valley and percent average steepness (i.e., slope); Appendix S2: Table S2). The best model

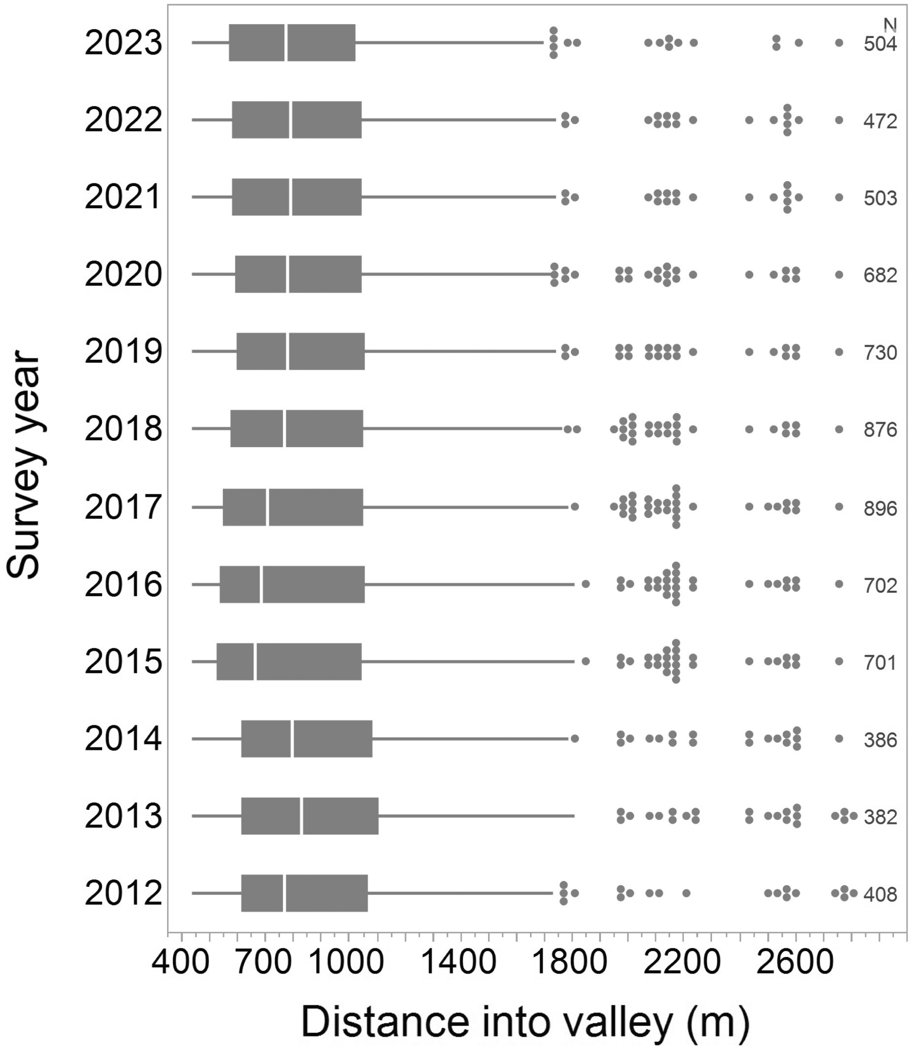

FIGURE 2 Median distance of live marked oak seedlings into the Hubbard Brook Experimental Forest, NH, over 13 years. The numbers on the right are the sample size for 25 m^2 plots occupied by live seedlings in that year. Box plots show where 50% of data lies with the shaded box, 95% of the data lies within the whiskers, and outliers are shown as individual dots beyond the whiskers.

matched the survival curve from Kaplan–Meier analysis with both results indicating a median seedling survival time of three to four years (Appendix S1: Figure S2). In the best model, the four covariables with the largest effect size included the following: year of germination, elevation, shrub cover, and seedling density (Figure 4; Appendix S2:

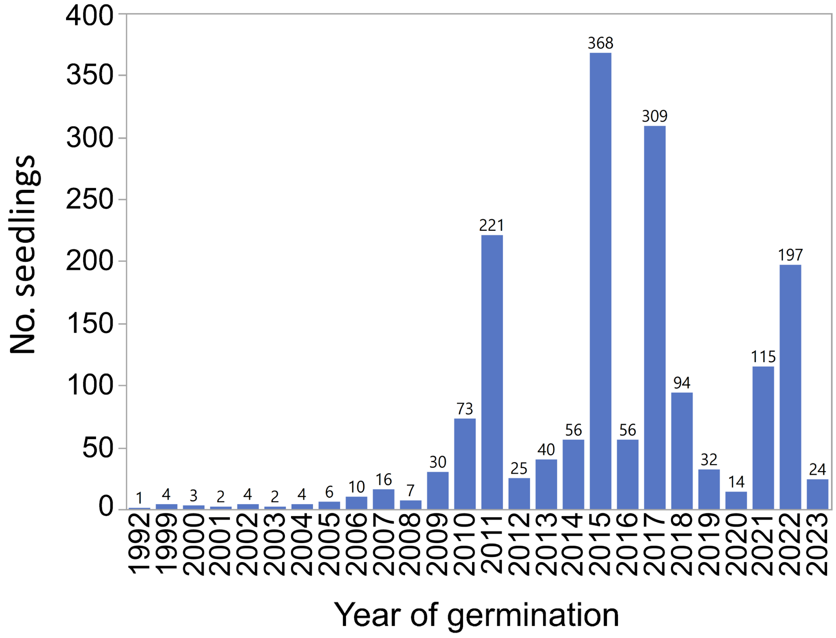

FIGURE 3 Annual influx of new seedlings on northern red oak study transects at Hubbard Brook Experimental Forest, NH, for 2011–2023. Seedling germination years for seedlings born before 2011 were assigned by counting back bud scars and only represent surviving seedlings. The numbers above the bars are the number of seedlings for each cohort year. $N = 1713$ as 20 seedlings could not be reliably assigned a birth year.

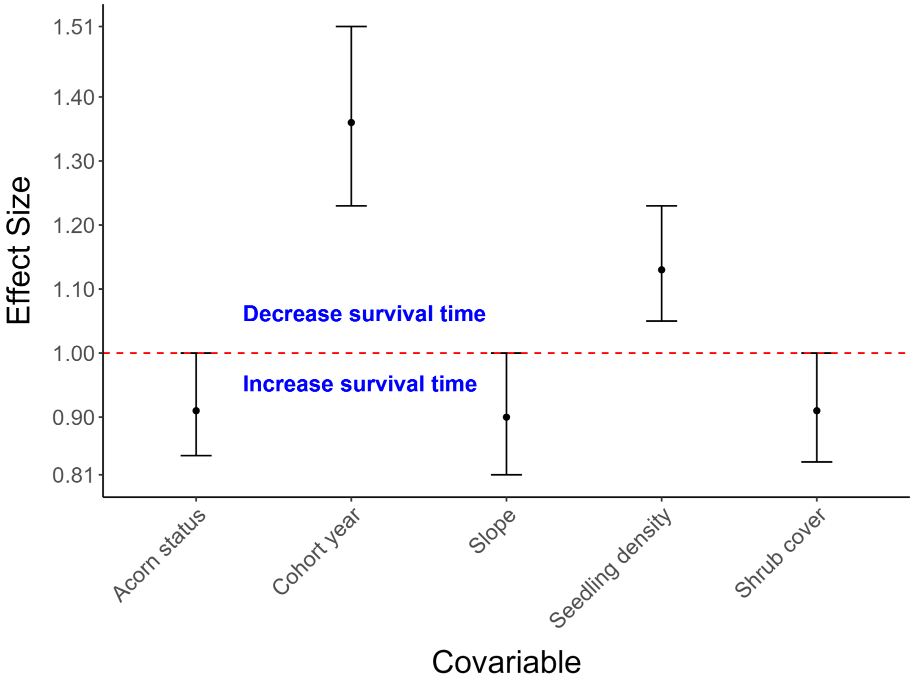

FIGURE 4 Estimated parameters for covariates that significantly impact the timing of seedling death within the reduced accelerated failure time model ($N = 937$). Parameter estimates (dots) with SE (bars) have been transformed with the exponential model to reflect the multiplicative acceleration/deceleration of survival time, where values below 1 increase the probability of survival, and values above 1 decrease the probability of survival.

Tables S3 and S4). The largest effect on seedling survival was the year of germination, which accelerated failure (i.e., decreased survival time) by a factor of 1.18 (95% CI: 1.09–1.29) indicating that seedlings born more recently survived for shorter periods of time than seedlings born closer to the start of the study (Figure 4; Appendix S1: Figure S5; Appendix S2: Table S5). Failure was decelerated (i.e., increased survival time) by a factor of 0.9 at higher elevations (95% CI: 0.82–0.98) and under higher shrub cover (95% CI: 0.83–0.98). Higher seedling density accelerated failure by a factor of 1.10 (95% CI: 1.02–1.18) (Figure 4).

Cohort seedling traits

Given the importance of cohort (year of germination), we considered differences in initial seedling traits between cohorts. For the subset of seedlings ($N = 937$) used for population survival analysis we wanted to explore cohort differences that might relate to seedling size differences between the 11 cohorts. Overall, median initial seedling height was 13.6 cm (interquartile range [IQR]: 11.2–16.0) and leaf number was 4 (IQR: 3–4) leaves (Table 3). The seedlings of the 2019 cohort had the shortest seedlings on average and they were significantly shorter than the average for seedlings of seven other cohorts. The seedlings of the 2014 and 2015 cohorts were shorter than four other cohorts (Table 3). There were overall differences between cohorts for leaf number with the 2018 cohort having fewer leaves than two cohorts, while the 2013 cohort had more leaves than five cohorts (Table 3). Most seedlings still had their acorn attached (78.9%), but there were significant differences between cohorts ($\chi^2 = 162.6$; df = 10; $p < 0.0001$). Moreover, the large influx years (2015 and 2017) had fewer acorns stolen while years with smaller cohorts (non-mast years: 2018, 2021, 2022) had a higher percent of seedlings with the acorn missing (Table 3). Initial height and leaf number were both positively correlated to increasing elevation and distance into the valley (Appendix S2: Table S2).

TABLE 3 Seedling traits by cohort year (year of germination) (median [interquartile range]) for northern red oak seedlings included in the population survival model for Hubbard Brook Experimental Forest, NH.

Cohort year	*N*	Vertical height (cm)	Number of leaves	Acorn attached (%)
2011	90	14.0 (12.4–16.5)	NA	88.9
2013	10	15.0 (13.7–17.6)	4 (2–4)[a]	100
2014	34	12.4 (10.6–15.1)[b]	4 (1–5)	91.2
2015	277	13.0 (11.2–15.5)[b]	4 (1–4)	89.9
2016	27	13.7 (10.8–16.1)	4 (1–4)	72.8
2017	237	14.3 (11.7–16.9)	4 (1–4)	89.5
2018	73	13.0 (11.3–15.6)	3 (1–4)[a]	41.1[c]
2019	21	10.6 (8.4–14.2)[b]	4 (1–4)	81.0
2020	6	12.5 (9.2–14.5)	4 (1–4)	66.7
2021	44	14.6 (12.5–17.1)	4 (2–5)	60.0[c]
2022	118	13.7 (10.7–16.6)	4 (1–4)	50.8[c]
All cohorts	937	13.6 (11.2–16.0)	4 (3–4)	78.9

[a] Overall test $\chi^2 = 17.3$; df = 9; $p = 0.04$. Wilcoxon posthoc ($\alpha = 0.05$) for cohort differences. The 2013 cohort had more leaves than 2014, 2015, 2016, 2018, and 2022. The 2018 cohort had fewer leaves than 2017 and 2021.

[b] Overall test $\chi^2 = 34.5$, df = 10, $p < 0.0002$. Wilcoxon posthoc ($\alpha = 0.05$) for cohort differences. The 2019 cohort seedlings were shorter than 2011, 2013, 2016, 2017, 2018, 2021, and 2022. The 2014 and 2015 cohorts were both shorter than 2011, 2013, 2017, and 2021.

[c] Overall test $\chi^2 = 162.6$; df = 10; $p < 0.0001$. ANOM for proportions ($\alpha = 0.05$ for cohort differences): 2018, 2021, and 2022 had more missing acorns.

Interannual variation and survival

Severe leaf damage (51% and above) varied from a low of 7.9% of seedlings in 2023 to a high of 20.7% in 2016. Overall, severe leaf damage was more common from 2015 to 2017 compared with recent years (Appendix S1: Figure S6). Growing season leaf damage agents were dominated by caterpillar herbivory in all years (2015–2022) which accounted for 74% of all leaf damage. The only other damage agents contributing to severe damage were fungal damage (14% in 2020) and rodent clipping (15% in 2016) (Appendix S1: Figure S7). We also left newly dead looking seedlings flagged to confirm death the next year. These seedlings were marked as “probably dead.” Only 6% of seedlings (66 instances) assessed as “probably dead” recovered and lived rather than being confirmed dead (1067 instances).

Much mortality occurred in the winter season with seedlings failing to break bud in the spring (Appendix S1: Figures S7 and S8). The 2019 season had the highest percentage (85%) of probably dead seedlings that failed to open their buds followed by 2018 (74.5%). It is likely that much of the rodent clipping also occurred under the snowpack. Within our study period, the winter of 2019 had the deepest, heaviest snowpack and 2016 the least snow (Appendix S1: Figure S9). There was internannual variation in seedling mortality with 2019 and 2020 being high mortality years and earlier years having the lowest mortality (Figure 5; Appendix S2: Table S6). The age of seedlings when they died also varied with the two oldest seedlings dying in 2019 (Appendix S1: Figure S10). Years following large seedling cohorts had lower age at death for the population reflecting the large number of

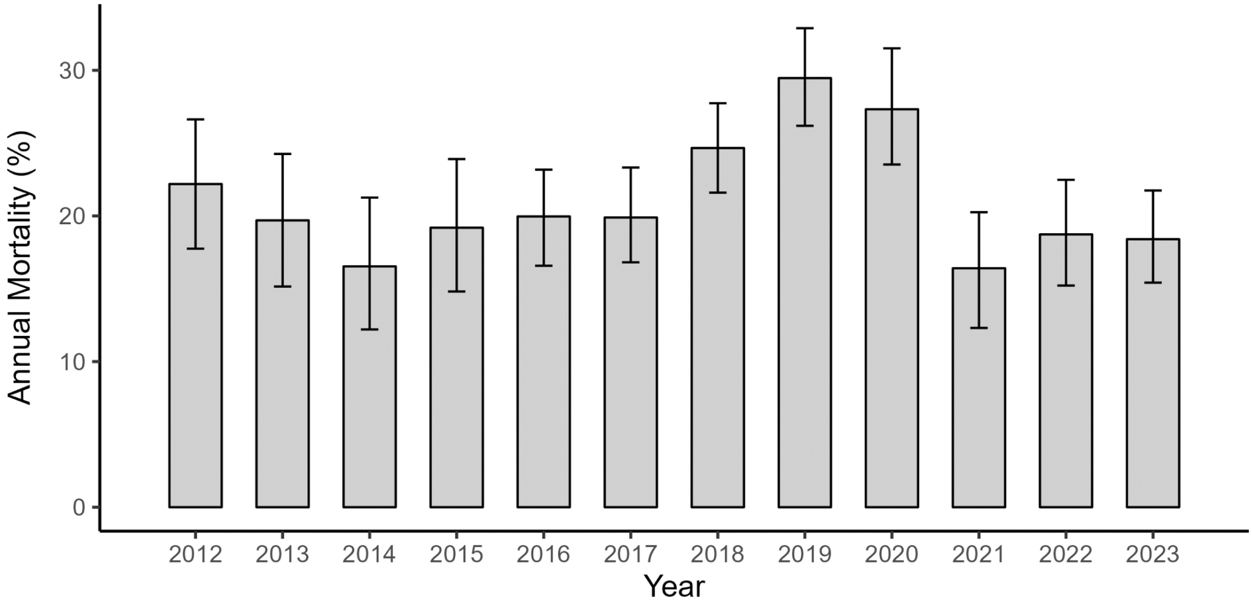

FIGURE 5 Seedling annual mortality of all ($N = 1733$) marked northern red oak seedlings in 24 study transects at Hubbard Brook Experimental Forest, NH. Error bars represent the 95% CI for annual mortality based on a binomial probability distribution.

first-year seedlings that die (Appendix S1: Figure S10). Overall, there was a significant, positive linear relationship between winter precipitation and annual seedling mortality ($F_{1,10} = 11.77$; $p = 0.0054$; Appendix S1: Figure S11).

On average, seedlings that died had been shorter, experienced a greater decrease in height, and had fewer leaves and branches in the previous season (Table 4; $N = 1580$). In addition, dead seedlings had a lower percentage of live branches and were more likely to have experienced severe leaf damage (Table 4). Of these condition metrics, models with leaf number and leaf damage better fit the pattern of seedling mortality (Table 5). The number of leaves was one of the best models in seven of the nine years, and having an additional leaf increased the likelihood of being alive by 1.5–2 times (Table 5). Leaf damage was among the best models in five of the nine years with different importance for the shift in leaf damage classes. The increased likelihood of death from leaf damage shift from 26%–50% to 51%–75%, was the most common with higher damage making seedlings 4–10 times more likely to die (Table 5). Seedling height was among the best models in one year, 2018, but had a small impact (1.1 times) on survival (Table 5).

DISCUSSION

During the 13-year period (2011–2023), we saw little evidence for expansion of QURU seedlings into the Hubbard Brook valley (Figure 2). The determinants of QURU seedling survival were complex for our multicohort sample. The short median lifespan of QURU seedlings (3–4 years; Appendix S2: Table S5) and the dynamic nature of seedling influx (Figure 3), both portray a population maintained mainly by input of new acorns. Seedlings appear to persist for around 20–30 years maximum as all five of the oldest seedlings marked in 2011 died during the course of the study (Appendix S1: Figure S10). The oldest marked QURU now alive is 22 years old. For seedlings recruited during the study, the year of germination was the strongest determinant of seedling survival time with more recently born seedlings dying sooner (Figure 4).

The shorter lifespans of more recent cohorts run counter to expectations with climate warming. The year of germination previously has been found to be an important determinant of survival in a comparison of three QURU seedling cohorts in Poland (Dyderski & Jagodziński, 2019). In our study, this pattern resulted from higher overall mortality later in the study, particularly in 2019 and 2020 (Figure 5). The increase in mortality in more recent years suggests less optimal conditions for QURU seedling establishment rather than predicted improving conditions (Iverson, Peters, et al., 2019).

Interannual climate variability is linked to particular years with higher mortality. The strongest evidence for this link comes from the co-occurrence of seedlings failing to break bud in the spring of 2019. The deepest, heaviest snowpack in the study period occurred in winter 2018–2019—a winter that was followed by the highest overall annual mortality (Figure 5). The continuing high mortality in 2020 may be explained by a combination of

TABLE 4 Differences in previous season seedling traits (mean [SE]) for seedlings that survived (Alive) and those that died (Dead).

Year	State	N	Height change (cm)	Height (cm)	Leaf number	Live branches (%)	Severe leaf damage[a] (%)
2023	Dead	101	−0.5 (0.5)	13.7 (0.6)	**3.1 (0.2)**[b]	77.2 (2.8)	**18.4**
	Alive	504	0.9 (0.2)	16.2 (0.3)	**4.0 (0.1)**	82.2 (1.2)	**4.0**
2022	Dead	81	−2.4 (0.6)	12.1 (0.8)	**2.8 (0.2)**	65.9 (3.4)	**31.2**
	Alive	537	−0.5 (0.2)	16.1 (0.4)	**3.8 (0.1)**	78.4 (1.4)	**5.8**
2021	Dead	61	−1.1 (0.6)	12.8 (0.8)	2.6 (0.2)	63.8 (4.1)	**27.0**
	Alive	428	0.4 (0.1)	16.9 (0.4)	3.8 (0.1)	74.9 (1.7)	**5.4**
2020	Dead	146	−0.2 (0.3)	13.3 (0.5)	**3.0 (0.1)**	74.8 (2.4)	14.2
	Alive	387	0.7 (0.2)	16.2 (0.3)	**4.0 (0.1)**	80.6 (1.4)	2.9
2019	Dead	201	−2.4 (0.4)	14.0 (0.7)	2.9 (0.1)	79.8 (1.9)	**16.1**
	Alive	526	−0.5 (0.2)	15.2 (0.3)	3.6 (0.1)	83.2 (1.2)	**3.3**
2018	Dead	182	−1.1 (0.4)	**13.3 (0.5)**	**3.3 (0.1)**	84.9 (1.8)	28.3
	Alive	672	−0.02 (0.2)	**16.1 (0.3)**	**3.9 (0.1)**	85.2 (1.1)	15.0
2017	Dead	113	−0.3 (0.3)	13.1 (0.5)	**2.6 (0.1)**	76.3 (2.5)	**31.2**
	Alive	746	0.9 (0.1)	16.5 (0.4)	**3.7 (0.1)**	82.4 (1.4)	**10.1**
2016	Dead	120	−1.4 (0.6)	13.9 (0.6)	**3.2 (0.1)**	88.5 (2.0)	23.2
	Alive	550	−0.1 (0.2)	15.4 (0.3)	**3.8 (0.1)**	88.8 (1.0)	14.7
2015[c]	Dead	58	−1.5 (2.0)	14.1 (1.9)	**3.1 (0.2)**		
	Alive	590	0.7 (0.2)	18.0 (0.6)	**4.3 (0.1)**		

Note: Results available for the nine most recent survey years. $N = 1580$.

[a] Leaf damage was analyzed as a categorical variable in the models but is summarized here as a percentage of all seedlings with 51% or more of the total leaf area damaged.

[b] Differences that had best fitted (largest deviance reduction) univariate logistic regression models differentiating dead and live seedlings for each survey appear in boldface. Model details are given in Table 5.

[c] Branch data and leaf damage were not recorded in 2014 resulting in fewer measures to predict 2015 season outcomes.

lagged effects of mechanical damage from snow and a 2020 drought event (Asbjornsen et al., 2022). QURU has been shown to be much less drought-tolerant in the seedling stage (Cavender-Bares & Bazzaz, 2000) and any preexisting leaf or root damage would exacerbate water stress (Wright et al., 1989). However, these correlations with the 2020 mortality peak are less clear than the impacts of winter snowpack. The importance of winter mortality in limiting QURU establishment merits further investigation.

Seedling traits

Patterns at the seedling scale depict individuals existing in suboptimal conditions unable to withstand loss of leaf area (Tables 4 and 5) and vulnerable to fatal damage under deep snowpack (Appendix S1: Figures S7, S8, and S11). Under such conditions, acorn removal also impacted survival time (Figure 4) and only 6% of seedlings were able to regrow after severe damage ("probably dead" status category). The maintenance of acorn attachment to the seedling increased survival time supporting the importance of initial seedling resources to establishment success (Figure 4). Although partially consumed acorns can germinate (Perea et al., 2011; Steele et al., 1993, 2001), they may have a disadvantage linked to lower survival. Acorn resources become more critical to establishment in suboptimal conditions (Badano & Sanchez-Montes de Oca, 2022). In addition to the loss of resources, seedlings with a missing acorn have also experienced the disturbance of having the acorn removed. The pattern of a higher percentage of acorns missing and presumably removed and eaten by rodents in non-mast years (Table 3) is consistent with the predator satiation hypothesis related to the evolution of masting (Janzen, 1971). The fact that in recent years, 2018 and 2022, about half of the seedlings had no acorn (Table 3) suggests that increased rodent activity may also be limiting oak establishment. However, with only a 13-year study window, we are limited in our ability to substantiate that events in more recent years are trends that could forecast the future.

Although initial seedling height and leaf number had low relative importance on population survivorship, the

TABLE 5 Univariate ordinal logistic regression models comparing effects of seedling traits in the season prior to the survey year on whether the seedling survived.

Survey year	Effect	df	Deviance reduction	Significance[a]	Impact of odds ratio
2015[b]	Leaves in 2014	1	9.75	<0.0001	1.6 times more likely to live with 1 more leaf
2016	Leaves in 2015	1	8.82	<0.0001	1.4 times more likely to live with 1 more leaf
2017	Leaves in 2016[c]	1	21.27	<0.0001	1.6 times more likely to live with 1 more leaf
	Leaf damage 2016[d]	4	19.84	<0.0001	2.7 times more likely to die with damage 2 versus 1
2018	Height in 2017	1	18.51	<0.0001	1.1 times more likely to live for 1 cm taller
2019	Leaf damage 2018	4	19.16	<0.0001	1.6 times more likely to live with damage 0 versus 1; 2 times more likely to die from damage 2 versus 1; 3.5 more likely to die from damage 3 versus 2
	Leaves in 2018	1	15.80	<0.0001	1.4 times more likely to live with 1 more leaf
2020	Leaves in 2019	1	17.62	<0.0001	1.5 times more likely to live with 1 more leaf
2021	Leaf damage 2020	4	14.46	<0.0001	6.3 times to die from damage 3 versus 2; 7.5 times for damage 4 versus 3
	Leaves in 2020	1	13.22	<0.0001	1.7 times likely to live with 1 more leaf
2022	Leaves in 2021	1	13.16	<0.0001	1.6 times more likely to live with 1 more leaf
	Leaf damage 2021	4	16.66	<0.0001	6.3 times more likely to die from damage 3 versus 2
2023	Leaf damage 2022	4	11.67	0.0001	5.2 times more likely to die from damage 3 versus 2
	Leaves in 2022	1	10.65	<0.0001	1.5 times more likely to live with 1 more leaf

Note: Sample sizes given in Table 4.

[a] The significance of the deviance reduction was tested by log-ratio using χ^2.

[b] Note the earliest survey year (2015) lacked data for branches and leaf damage.

[c] Univariate models with similar deviance reduction (<2) were considered equally plausible.

[d] Leaf damage was scored on a five-point scale (0–4, with 0 being <5% damage and 4 being >76% damage).

condition of specific seedlings, particularly leaf conditions (number and damage) in the previous season, differed between seedlings that died the following year (Tables 4 and 5). In other words, initial conditions (those measured in the population survival analysis) are less important than the year-to-year conditions in terms of survival effects. The small effect of initial seedling height and leaf number in the population model can be explained further by minimal differentiation between cohorts for these measures initially, that is, most first-year seedlings averaged 12–14 cm in height with 3–4 leaves (Table 3). In addition, although leaf damage clearly had an impact on interannual survival (Tables 4 and 5), the number of seedlings experiencing severe leaf damage during the growing season was typically low (15% or less; Appendix S1: Figure S6) and less than 20% of all deaths that occurred during the growing season (Appendix S1: Figure S8).

Plant community covariables

Shrub cover and initial seedling density were important plant community covariables that influenced survivorship (Figure 4; Appendix S2: Table S4). Although high shrub cover may have a significant negative effect on QURU survival by decreasing light availability (Kern et al., 2012), more studies have found shrub cover to provide protection against herbivory or frost, thereby improving survival (Buckley et al., 1998; Woziwoda et al., 2018). Shrubs could also provide physical protection for seedlings, by hiding them from herbivores (Woziwoda et al., 2018) or by buffering against winter climate effects such as physical damage from snowpack. The relevance of winter mortality in this study suggests lessening of mechanical damage from snowpack may be a critical benefit of shrub cover deserving of future study.

The importance of seedling density for seedling survival time is consistent with the concept of conspecific negative density dependence, which has been found increasingly in both tropical and temperate trees and is thought to maintain diversity (Comita et al., 2014). The mechanisms of pathogen and pest escape further away from conspecifics has been found in previous work on QURU seedlings (Jevon et al., 2022). In our study, oak seedling densities were fairly low though highest after the influx from mast cohorts. Therefore, the effect of seedling density on seedling survival in this study more likely resulted from a combination of higher mortality for first-year seedlings (Appendix S1: Figure S10) and intense competition for seedlings occurring in clumps (10% of all seedlings).

Surprisingly, light transmission was not significantly related to seedling survival. The overall lack of significance of light transmission in our study seemingly is at contrast with the critical importance of light to QURU regeneration in many other studies; however, the universally low light transmission in our plots (Table 2) was in a range that had no impact on QURU seedling biomass or biomass allocation (0%–12%; Dyderski & Jagodziński, 2019). These low light levels likely represent the suboptimal growth conditions that make leaf number, leaf damage and acorn loss so impactful for life and death (Tables 4 and 5).

Terrain covariables

A number of terrain variables are tightly related to the distance into the valley because elevation and steepness increase together, and elevation is highly correlated to distance into the valley (Figure 1; Appendix S2: Table S2). In addition, plant community variables of percent hemlock and percent light transmission also change with both distance into the valley and elevation (Appendix S2: Table S2). And thirdly, QURU presence as both adults and seedlings drops off quickly with distance into the valley (Figure 1; Appendix S1: Figure S3). That elevation had an important effect on population seedling survival is therefore likely related to a whole suite of changing factors. The positive impact of elevation on survival was unexpected. One possible scenario is for larger acorns to be dispersed further, which could result in seedlings that begin with more resources and are larger initially. Both initial seedling height and leaf number were positively correlated to both distance into the valley and elevation (Appendix S2: Table S2). Given the relationship between seedling density and decreased survival time, the decrease in seedling density with elevation may also partially explain the positive impact of elevation on survival in our study. Although the interpretation of elevation's effect is not clear, prolonged survival in higher elevation plots further into the valley could promote QURU expansion in the future.

Seedling expansion

For both distance of seedlings into the valley, and of plots with more than one seedling establishment event, the median distance was 800 m suggesting that seedling expansion is at a standstill (Figure 2; Appendix S1: Figure S4). Overall, the median survival time of 3–4 years and the rapid turnover of the QURU seedling population suggest the lack of expansion into the valley results in large part from poor seedling survival. In addition, several lines of evidence support continuing suboptimal conditions for QURU establishment in the understory of the northern hardwood forest: no seedlings beyond 30 years old persist; leaf loss and damage greatly increased the probability of dying; loss of acorn resources shortens seedling lifespan; and many seedlings fail to survive the winter. Failure to survive the winter may be from direct stem damage caused by snowpack or indirectly from lack of carbon reserves (Canham et al., 1999). Further work would be needed to separate these possible causes and their relative importance. Canham et al. (1999) found that even with complete defoliation, seedlings rarely died in the growing season, which agrees with our observations over a longer time frame. The lack of QURU seedling progression farther into the valley is also consistent with the limited dispersal of acorns reported from studies in Québec (García & Houle, 2005) and in North Carolina (Moran & Clark, 2012). However, the spatial stasis of the temporally dynamic population of tree seedlings studied here seems imminently limited by the prevalence of suboptimal growth conditions punctuated by damaging climate events.

The large uncertainties of successful migration in response to climate change have led to the suggestion of assisted migration for QURU (Iverson, Prasad, et al., 2019; Rauschendorfer et al., 2022). However, acorn planting often meets with large losses to rodent predation (Villalobos et al., 2020). Several case studies of assisted migration for population expansion of QURU in New England have used planting of young trees with good initial survival (Clark et al., 2022; Palik et al., 2022). Studies from Europe where QURU has become invasive suggest that escape from pests and pathogens has been important to QURU invasiveness (Dyderski et al., 2020). Such a mechanism may play an important role in migration of QURU in North America if there is at least temporary escape from pests and pathogens at migration fronts. In addition, our study emphasizes the importance of interactions between patterns of seed input and interannual climate variation on QURU seedling survival and potential establishment. In particular, the role of snowpack and drought conditions in impeding QURU expansion requires further attention.

Despite climate conditions at HBEF that are warming and include annual temperatures within the comfort zone of QURU (8°C; Cogbill et al., 2002), there is little evidence of local population expansion as yet. The QURU seedlings appear to have relatively fast turnover (median age 3–4 years) that reflects sub-optimal conditions as indicated by fatal repercussions for both loss of leaf area and acorn resources. Uniformly low light levels (≤10% transmittance) recorded for our study plots are known to be too low to elicit QURU growth responses (Dyderski & Jagodziński, 2019). The ability of QURU to persist in suboptimal conditions is promoted initially by considerable seed resources (Brose, 2011; Canham et al., 1996) and the persistence of our QURU seedling population appears highly dependent on acorn input. In addition, we posit based on the strong temporal relationship between seedling mortality and heavy snowpack that snowpack depths may play a key role in limiting QURU establishment in the northern hardwoods.

AUTHOR CONTRIBUTIONS

Natalie L. Cleavitt conceived the project, was involved in all years of fieldwork, and led paper writing and revisions. John J. Battles and Jaclyn Hatala Matthes led the accelerated failure time analysis. Jaclyn Hatala Matthes advised Sage Wentzell-Brehme, who completed a senior thesis based on the project and was involved in fieldwork in 2019 and 2021. John J. Battles led work on canopy photography in the field and lab analysis stages. All authors contributed to manuscript construction.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Cleavitt, 2024; Cleavitt & Battles, 2024) are available from the Environmental Data Initiative: 10.6073/pasta/1de25c7fd5bc23dc39171d66b29652ac; 10.6073/pasta/1030af44239528ce4e17f7f585d00462.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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