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RESEARCH ARTICLE

Canopy gaps facilitate upslope shifts in montane conifers but not in temperate deciduous trees in the Northeastern United States

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Abstract

1. Many montane tree species are expected to migrate upslope as climate warms, but it is not clear if forest canopy gaps, which can facilitate tree seedling recruitment, serve as an important mechanism driving tree species range shifts. Patterns of tree seedling establishment can inform us about early stages of tree species migrations and are critical to examine in the context of global climate change.
2. We contrasted elevational distributions of tree seedlings both within and outside of forest canopy gaps with the distributions of conspecific adults and saplings across the deciduous-coniferous ecotone on ten mountains in four states of the Northeastern United States. We tested if seedling distributions of four dominant tree species (*Abies balsamea*, *Picea rubens*, *Acer saccharum* and *Fagus grandifolia*) were shifted upslope of conspecific adult and sapling distributions. We also examined if this shift was facilitated by canopy gaps and what environmental drivers affected species distributions.
3. There was limited seedling recruitment of dominant tree species at the temperate-coniferous ecotone, which we attributed to (i) an observed downslope shift of seedling distributions of the low-elevation deciduous species (*Acer saccharum*, *Fagus grandifolia*) and (ii) an upslope shift in seedling distributions of the high-elevation conifers (*Abies balsamea*, *Picea rubens*). The upslope shift of conifer seedlings contrasts with our previous research at these sites which observed downslope shifts of sapling distributions in *Picea rubens*, suggesting that seedlings may be responding to more recent climate warming. Canopy gaps in high-elevation conifer forests facilitated these upslope shifts by promoting conifer seedling recruitment. However, gaps at lower elevations did not play a significant role in seedling recruitment or the observed downslope shifts of the dominant deciduous species. Climate was the dominant predictor of adult tree distributions whereas both climate and soil were important predictors of seedling distributions.

4. *Synthesis.* Our study illustrates that tree seedlings have the potential for monitoring the early stages of tree species migrations, and particularly so in canopy gaps in high-elevation conifer forests. Further, we stress that species range shifts are sensitive to local scale heterogeneity in light availability (i.e. canopy gaps) and other non- climatic factors.

KEYWORDS

biogeography, forest gaps, global change ecology, northern hardwood forest, seedlings, spruce- fir forest, tree distributions

1 | INTRODUCTION

Global climate change has been increasingly suggested as an important driver behind the well- documented ongoing shifts in species distributions on both regional and global scales (Pecl et al., 2017; Scheffers et al., 2016). Even more substantial changes in species distributions are expected to occur over the next 100 years as climate continues to change (e.g. Prasad et al., 2020). Tree species are especially susceptible to delayed changes in their distributions given their slow growth, relatively low dispersal ability, and long lifespans that can lead to slow population turnover and potentially low ability to adapt to rapidly changing climate (Aitken et al., 2008; Miller & McGill, 2018). Trees perform a wide array of important ecosystem services including nutrient cycling, carbon sequestration, and habitat provisioning (e.g. Beck et al., 2011; Ellison et al., 2005; Likens et al., 1970), thus, a better understanding of tree population responses to changing climate is of paramount importance.

Given slow population turnover, the early stages of distributional shifts of tree species have often been studied by analysing demographic changes in tree populations along latitudinal and elevational climatic gradients that are particularly sensitive to changing climate (e.g. Lenoir et al., 2009; O'Sullivan et al., 2021; Wason & Dovciak, 2017; Zhu et al., 2012). These spatial climatic gradients are often superimposed over variable disturbance regimes as well as edaphic and other factors (e.g. land use history, soil depth) that can affect species range shifts (Brown & Vellend, 2014; Harsch et al., 2009; Jump et al., 2009; Lee et al., 2005). While prevailing theory suggests that tree species track changing climate by shifting their range limits to higher elevations (upslope) or higher latitudes (Beckage et al., 2008; Janowiak et al., 2018), some species have been shown to be shifting in an opposite direction; toward warmer climate (downslope or to lower latitudes) often due to past disturbance history and ongoing successional processes (Fei et al., 2017; Foster & D'Amato, 2015; O'Sullivan et al., 2021; Wason & Dovciak, 2017). For instance, Wason and Dovciak (2017) posited that an observed downslope shift of red spruce may have been the result of postharvest successional dynamics at lower elevations. Other studies have noted very slow or delayed range expansion due to other limiting factors (Alexander et al., 2018; Liang et al., 2018; Sittaro et al., 2017; Zhu et al., 2012). However, it is important to note that many studies that examine species distribution shifts focus solely on dynamics occurring on range margins rather than across the entire range of tree species within the forest interior (but see Dirnböck et al., 2011; Ruiz-Labourdette et al., 2012).

While the latitudinal or elevational gradient studies of tree demography in forest ecosystems tend to employ large datasets to document robust patterns, they tend to average out environmental heterogeneity which can affect where juvenile trees can successfully establish and survive (cf. windows of opportunity; Dovčiak et al., 2005). Although relatively rare, forest canopy gaps caused by disturbance (e.g. windthrow) are an important source of environmental heterogeneity in forests as they create open (relatively high- light) microsites that act as nurseries for the establishment and recruitment of tree seedlings (Muscolo et al., 2014; Pham et al., 2004; Rentch et al., 2010; Runkle, 1981; Sprugel, 1984). Moreover, climate warming tends to affect the microclimate (higher daytime temperatures) in forest gaps more so than under closed canopies that maintain cooler microclimates by preventing solar radiation from entering the forest interior (de Frenne et al., 2019; De Lombaerde et al., 2022). In cold montane environments with short growing seasons, we expect that the warming effect of gaps is likely to be a net positive for tree establishment (Fisichelli et al., 2014). The dual effect of increased light availability and higher daytime temperatures in gaps could alleviate the environmental stress imposed on species at the cold edge of their range at higher elevations (Leithead et al., 2010). Thus, canopy gaps can facilitate tree species range shifts and they have great potential for monitoring the early stages of climate- induced tree species migrations. Although the idea that disturbance can generally facilitate or inhibit tree species range shifts has been recently strongly corroborated (Brice et al., 2020; Liang et al., 2018), the impact of fine- scale gap- phase dynamics (cf. Runkle, 1981; Sprugel, 1984) on climate- change driven tree species range shifts has not been fully explored.

Forest gaps are particularly important for tree seedlings, a critical life stage in tree development, as tree seedlings tend to have high mortality rates and specific (and often narrower than adults) ecological niches (cf. regeneration niche, Grubb, 1977; Leck et al., 2008). As a result, tree seedling survival is more sensitive to environmental variation (e.g. in climate or soils) than the survival of older individuals (e.g. saplings or mature trees), allowing for a decoupling of these demographic stages in space (Dovčiak et al., 2001; Lenoir et al., 2009). Importantly, contemporary tree seedling populations in forest understories were established under more recent (and thus warmer) climatic conditions as opposed to older tree life stages that were established earlier under a previous somewhat cooler climate (cf. NOAA National Centers for Environmental Information, 2022), which is especially apparent

for shade- tolerant species with saplings that may remain suppressed in the understory for decades (Wason & Dovciak, 2017). Consequently, climate-induced changes in tree species ranges should be detected first by changes in tree seedling composition in canopy gaps, and this should indicate that seedling distributions may be more sensitive to climate per se than edaphic or topographical factors (see Wason & Dovciak, 2017). Studying the effects of changing climate on tree recruitment in this way is a novel approach and is an important research priority as these processes add substantial uncertainty in predicting responses of tree species ranges to climate change (Copenhaver- Parry et al., 2020; Heiland et al., 2022).

In order to improve our understanding of the unexplored role of gap-phase dynamics in climate- induced tree species range shifts, we collected data on tree seedling distributions and established vegetation plots in forest gaps and under forest canopies along montane slopes in the Northeastern United States. This research is an expansion of our previous work contrasting the distributions of saplings to adult conspecifics within the same system (cf. Wason & Dovciak, 2017). We generated hypotheses addressing three primary areas of interest: (1) the contrast between seedling distributions and previously measured sapling and adult conspecific distributions; (2) the role of canopy gaps in potentially facilitating species range shifts as detected in the seedling stage and (3) the relative importance of various environmental factors on species distributions for all life stages. First, given that seedlings were established more recently under warmer climate conditions, we hypothesised that seedlings would display overall upslope shifts in their distributions relative to the distributions of conspecific adults and saplings (hypothesis 1, H1). Second, we hypothesised that seedling distributions would be positively affected by canopy openness due to increased light availability and warmer temperatures at the cold edge of their ranges, and thus, they would be shifted upslope of adult distributions more so in canopy gaps than under closed forest canopies (hypothesis 2, H2). Lastly, since seedlings were established under a warmer recent climate, we hypothesised that compared to conspecific adults or saplings, variation in seedling distributions would be better explained by current climate conditions (e.g. temperature, precipitation, vapour pressure deficit) and less so with soils (e.g. pH, soil organic matter, soil depth to bedrock), and landform (e.g. slope, aspect; hypothesis 3, H3).

2 | MATERIALS AND METHODS

2.1 | Study area

Our study was carried out across four states in the Northeastern United States (New York, Vermont, New Hampshire, and Maine) in a broad region known as the Adirondack- New England highlands (cf. Bailey, 1995). These forest ecosystems represent a regional transition from the temperate broadleaf deciduous forest biome in the south to the boreal evergreen conifer forest in the north (Bailey, 1995). Soils are rocky spodosols and the climate is continental with warm summers and cold, snowy winters; mean annual temperatures range between 3 and 11°C across the region, mean length of the frost- free period is ~100 days, mean annual snowfall is above 2550 mm, and the mean annual precipitation of ~890 mm is evenly distributed throughout the year (Bailey, 1995).

The region is characterized by a highly dissected terrain and distinct elevational vegetation zones with northern hardwood (broadleaf deciduous) forests generally occurring below ~800 meters above sea level (a.s.l.) and evergreen coniferous forests occurring at higher elevations (cf. Cogbill & White, 1991; Wason & Dovciak, 2017). The northern hardwood forests at lower elevations are dominated by sugar maple (*Acer saccharum* Marshall), yellow birch (*Betula alleghaniensis* Britton), and American beech (*Fagus grandifolia* Ehrh.), while the high- elevation conifer forests are dominated by red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea* (L.) Mill.) as they transition to balsam fir krummholz (at ~1100 to 1400 m a.s.l.) and ultimately to alpine meadows at the highest elevations (Cogbill and White, 1991; Bailey, 1995; Wason & Dovciak, 2017). The region has experienced significant climate warming (Janowiak et al., 2018), soil acidification linked to atmospheric deposition of sulfur and nitrogen (Driscoll et al., 2001), and extensive logging prior to the early 1900s (White & Cogbill, 1992). Additional details on the study region are found in Wason and Dovciak (2017).

2.2 | Study design

We selected ten study mountains across the region to quantify the demography and distribution of forest tree species across climatic gradients of the Northeastern United States (Figure 1). The mountains were selected to include elevations from 500 to 1000 m a.s.l. in order to capture the full transition from northern hardwood forests at low elevations to spruce- fir forests at high elevations (Table 1). Most of the selected mountains had a protected status (e.g. Adirondack Forest Preserve) and we specifically selected areas within them that had mature forests with ongoing natural gap- phase dynamics (cf. Beeles et al., 2022; Wason & Dovciak, 2017). Relevant research permits were obtained from the Vermont Department of Forests, Parks and Recreation (#21089), the New Hampshire Division of Forests and Lands (#13- 003), the Maine Department of Agriculture, Conservation and Forestry (#2019- 004), the Green Mountain National Forest (#4000) and the White Mountain National Forest (#2720). Further permissions were granted by the Forest Ecology Monitoring Cooperative and Dartmouth College.

In 2013, we established five or six 225 m long transects (hereafter referred to as sites) on each study mountain along contour lines systematically at 100 m intervals in elevation, starting in the northern hardwood forest at 500 m a.s.l. whenever possible and ending in spruce- fir forest (1000 m a.s.l.). In a few cases, appropriate mature forest stands could not be located at 500 m a.s.l., and the lowest aPredicted values.

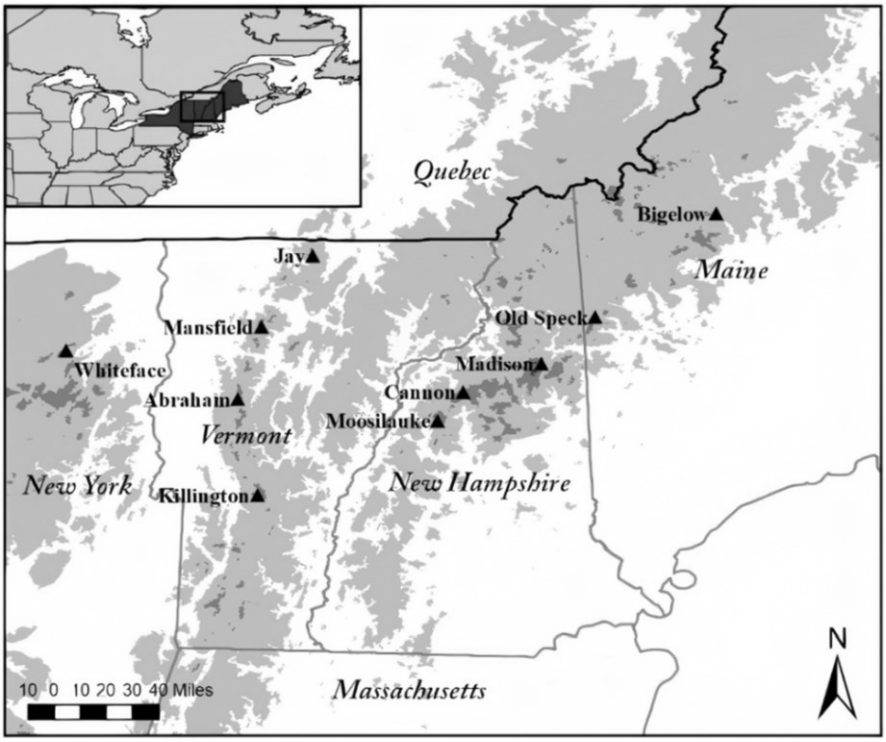

FIGURE 1 Locations of the 10 study mountains (marked with black triangles) in the Northeastern United States. Unshaded (white) areas on the map indicate elevations <500 m a.s.l., light grey areas represent elevations between 500 to 800 m a.s.l. and dark grey areas represent elevations >800 m a.s.l. Thick lines show national (US- Canada) and thin lines show US state borders.

TABLE 1 Summary information for each of the 10 study mountains in the Northeastern United States. Mean ecotone elevations (±SE) were calculated from predicted deciduous and conifer basal areas by Wason et al. (2017), growing degree days (GDD) were calculated for each elevation (transect) from iButton temperature data following Gavin et al. (2008) and Wason and Dovciak (2017), and soil depths are site means of soil probe measurements. Thirty-year means (1980– 2010) for annual means of daily minimum and maximum vapour pressure deficit (VPDmin and VPDmax, kPa), temperatures (Tmin and Tmax, °C) and total annual precipitation (PPT, cm) are based on PRISM gridded climate data (PRISM Climate Group, OR). Soil pH and soil organic matter content (SOM, %) are transect means of aggregated soil core analyses for the subset of four relatively more accessible study mountains.

Mountain	Summit elevation (m)	Ecotone elevation (m)	GDD range (°C)	VPD range (kPa)	Temperature (		Mean PPT (cm)	Soil depth range (cm)	pH range	SOM range (%)
					Min	Max				
Abraham	1207	790 (±27)	1169– 1676	0.6– 7.3	−1.7	10.7	130	24– 39	3.3– 5.7	3.7– 73.9
Bigelow	1227	621 (±46)	1069– 1662	0.7– 7.2	−3.1	9.1	100	22– 46	3.4– 4.6[a]	14.4- 74.9[a]
Cannon	1228	786 (±31)	1218– 1538	0.7– 7.9	−1.5	10.4	121	13– 56	3.7– 4.0[a]	14.9- 60.8[a]
Jay	1148	824 (±36)	1201– 1765	0.6– 6.6	−1.5	9.3	139	17– 41	3.3– 4.1	5.9– 73.4
Killington	1288	896 (±26)	1155– 1650	0.6– 7.3	−1.8	11.6	137	14– 38	3.1– 4.9	4.5– 92.8
Madison	1620	849 (±34)	1277– 1671	0.6– 8.2	−2.6	10.8	166	16– 38	3.6– 4.6[a]	14.6- 55.2[a]
Mansfield	1337	752 (±65)	1240– 1467	0.6– 6.3	−1.3	10.4	149	13– 67	3.3– 4.2	10.1– 88.5
Moosilauke	1468	734 (±79)	1162– 1515	0.7– 7.8	−1.9	10.5	122	19– 56	3.6– 4.7[a]	14.9- 72.6[a]
Old Speck	1263	681 (±50)	1014– 1564	0.7– 7.8	−2.9	9.9	120	23– 36	3.6– 4.9[a]	15.4- 55.2[a]
Whiteface	1483	~800	1200- 2000	0.5– 7.8	−1.9	11.4	118	25– 60	3.7– 4.9[a]	14.4- 85.2[a]

elevation site was then established at 600 m a.s.l.; thus, a total of 57 sites were established across the 10 mountains. In 2019, we located five canopy gaps adjacent to each site (within 50 m horizontal) in order to survey tree seedling populations growing in these more open conditions. Gaps were defined as areas with an average of >20% canopy openness (taken from three densiometer measurements). We surveyed tree seedling populations on understory vegetation plots (1 × 1 m large) placed systematically at each site both along the transects and in newly established canopy gaps in 2019; 15 of these plots were established along each transect at 15 m intervals (non- gap plots) and another 15 plots were established across the five canopy gaps (gap plots) associated with each transect (three plots per gap; located in the center and on the northern and southern edges of each gap).

2.3 | Field surveys and measurements

Overstory trees were surveyed using the point- centre-q uarter method at each site using non- gap vegetation plots as sampling points (Cottam & Curtis, 1956; Holway et al., 1969; Wason & Dovciak, 2017), which allowed for the quantification of relative basal area, relative frequency and relative stem density by species for adult canopy trees and saplings. Adult trees were defined as individuals >10 cm diameter at breast height (DBH) and saplings were defined as individuals <10 cm DBH. We used a 10 cm DBH threshold to represent trees transitioning from subcanopy to canopy positions, as defined by Battles et al. (1992) from research done on Whiteface Mountain, NY. From the centre of every fifth vegetation plot we also recorded slope, aspect and average soil depth to bedrock (using a metal soil depth probe; see Wason & Dovciak, 2017).

Tree seedlings (defined broadly as juvenile trees <2 m tall) were surveyed on all understory vegetation plots by counting the number of seedlings by species and seedling size class (class 1 = seedlings <50 cm tall, class 2 = seedlings >50 cm and < 100 cm tall, class 3 = seedlings >100 cm and < 200 cm tall). However, since the majority (~90%) of all seedlings fell into size class 1, we ultimately pooled all the seedlings into a single seedling size class (<2 m tall) for the analyses. To characterize understory light environment of tree seedlings, we measured canopy openness with a densiometer (Type A Convex Spherical Densiometer; Forestry Suppliers Inc.) at 1 m height above the ground at the centre of all understory vegetation plots.

Climatic measurements (air temperature, humidity) were carried out using iButton dataloggers (model DS1923; Maxim Integrated Products, Inc.) mounted 1 m aboveground and recording every two hours for approximately 1 year (spring 2013 to spring 2014). At each site, one iButton was deployed at the centre of each site (at the central non- gap plot). Each iButton was equipped with a white plastic shield with ventilation holes to protect from direct solar radiation and facilitate airflow (Wason & Dovciak, 2017).

Lastly, we characterized soil environment more fully on a subset of four relatively more accessible mountains (Abraham, Jay, Killington, and Mansfield) by collecting six soil cores (each 20 cm deep and 10 cm in diameter) at each site (a total of 4 mountains × 6 sites × 6 cores = 144 soil cores). All soils were kept cold during transport and processed to isolate the upper B soil horizon. All soils were sieved using a 2 mm sieve to remove large debris. Sieved soils were processed to quantify soil pH via electrometric methods, and soil organic matter (SOM) via the loss on ignition procedure in the Soil Analysis Laboratory at SUNY- ESF following Carter and Gregorich (2007).

2.4 | Derived predictor variables

To contrast the ecological drivers of seedling, sapling and adult distributions, we compiled climate, soil and landform variables for each site, both from our 2019 field measurements (see above) and from online national climate databases available for the region (Table 1). Long- term climate variables for each site were extracted from 800- meter resolution PRISM 30- year normal data (1981– 2010; PRISM Climate Group, Oregon State University, https://prism. oregon state.edu). These included annual minimum and maximum temperatures, total annual precipitation, and annual minimum and maximum vapour pressure deficits (VPD; all calculated from daily values of temperature and VPD minima and maxima by the PRISM Climate Group). In addition, we calculated growing degree days (GDD) from our field iButton temperature measurements to approximate local growing season length and warmth at each site following Gavin et al. (2008) and Wason and Dovciak (2017).

Site means were calculated from the field measurements of soil variables that included soil depth, pH and soil organic matter (SOM). Since soil pH and SOM were not measured on some mountains, we estimated them from known elevation values using the mice function (Multivariate Imputation by Chained Equations) in R (R Development Core Team, 2019) given the similarities in regional geology and the strong linear relationship between elevation and the two soil variables (pH: $R^2 = 0.91$, $p = 0.003$; SOM: $R^2 = 0.86$, $p = 0.008$, Figure S1). Missing values were estimated using predictive mean matching and a total of five datasets were created to average the final missing values (Little, 1988; Figure S2).

Finally, we calculated site means for the landform variables— slope and aspect— that can influence light and other resource levels for plants. Aspect was rescaled following McCune and Keon (2002) in order to make it a linear rather than a circular variable:

$$180 - |\text{Aspect} - 180| \quad (1)$$

Comparisons of correlation coefficients between all pairs of variables and variance inflation factors (VIF) for all variables resulted in the removal of maximum and minimum annual temperature from consideration in linear mixed models (VIF values for the remaining variables in the models were <4 and deemed acceptable; Belsley et al., 2005). GDD (representing temperature) was included as a predictor in all final models.

2.5 | Statistical analyses

Our analyses generally followed modelling approaches in Wason and Dovciak (2017) and Lenoir et al. (2009). We focused on four regionally dominant shade- tolerant species (sugar maple, American beech, balsam fir, and red spruce) and three broad demographic classes: seedlings (<2 m tall), saplings (>2 m tall and < 10 cm DBH), and adult canopy trees (>10 cm DBH; cf. Wason & Dovciak, 2017).

In order to test if species seedling distributions shifted upslope of conspecific sapling and adult tree distributions (hypothesis H1), we constructed logistic regression models for species occupancy along the elevational gradient (500– 1000 m a.s.l.) separately for each demographic class (seedlings, saplings, and adults) of each species on each study mountain. Following Canham and Thomas (2010), we characterized species elevational distributions using species relative frequency (rather than relative density). Species relative frequency (probability of occupancy) was calculated for each species and demographic class as the proportion of plots occupied at each elevation (out of 30 plots in total distributed along the transect and in gaps, see *Study Design*). Species importance values, which was used in additional analyses (see below), were computed as the site-level average of species relative frequency and relative density (relative basal area was not used as this could not be applied to seedlings; Holway et al., 1969; Siccama, 1974). In order to test if species seedling distributions shifted upslope more in gaps than under forest canopies (hypothesis H2), we calculated seedling relative frequencies separately for the 15 gap and 15 non- gap plots at each elevation, and constructed separate logistic regression models for species seedling occupancy along the elevational gradient for gaps and under the canopy (non- gap seedlings).

Once the logistic regression models for species occupancy across elevations were constructed for each mountain, species, demographic class, and seedling canopy environment (gap vs. non- gap), we calculated the elevation mismatch of any two demographic classes of interest for each species and mountain based on Lenoir et al. (2009) and Wason and Dovciak (2017) as follows. First, demographic elevational mismatches were calculated only for those mountains where (i) the species was present at two or more elevations, and (ii) the species exhibited a distributional peak or upper or lower range margin. We calculated the elevation of species peak probability of site occupancy for red spruce – a species with its entire range within our study elevations. For species where we captured mostly the upper elevation range (American beech, sugar maple) or the lower elevation range (balsam fir), we calculated the elevation of species transition to or from dominance (species probability of occupancy = 0.5; see Figures S3 and S4). We then calculated the elevation mismatch between demographic classes (e.g. adults vs. all seedlings; adults vs. saplings; adults vs. gap or non-gap seedlings) by subtracting the elevation of the peak of occupancy (or margin) of adults from that of seedlings or saplings. Thus, positive elevation mismatch values would indicate upslope seedling shifts relative to adults (consistent with hypothesis H1, consistent with H2 if found only for gap seedlings), while a negative elevation mismatch values would suggest a downslope seedling shift (inconsistent with either H1 or H2). We statistically tested hypotheses H1 and H2 for each species by testing whether the mean demographic elevation mismatches across all studied mountains were significantly different from zero using one sample t- tests. In addition, we used linear models to verify the underlying assumption that tree seedling distributions responded to forest gaps (hypothesis H2) by testing (i) if seedling species importance varied with canopy openness and (ii) if canopy openness varied with elevation, given that forest gaps all had higher canopy openness values than non- gap environments.

Finally, in order to test if climate had a greater role in controlling the distribution of seedlings than the distributions of conspecific adults or saplings (hypothesis H3), we tested how individual predictor variables from three broad predictor categories— climate, soil, and landform (Table 2)—

TABLE 2 Abbreviations and definitions of the predictor variables (by category) used for modelling distributions of tree seedlings, saplings, and adults on elevation gradients in the Northeastern United States based on species importance values (average of species relative frequency and density). VPDmin, VPDmax, Tmean and PPT were based on PRISM 30- year normal data (i.e. 30- year means of annual values). Remaining variables were based on field measurements (site means). GDD^2 was used to account for the peak in the distribution of red spruce in mid- elevations (cf. Wason & Dovciak, 2017).

Category	Variable	Description
Climate	GDD	Growing degree days (°C)
	GDD^2	Growing degree days (squared)
	VPDmin	Mean annual minimum vapour pressure deficit (Kpa)
	VPDmax	Mean annual maximum vapour pressure deficit (Kpa)
	Tmean	Mean annual mean temperature (°C)
	PPT	Mean annual precipitation (cm)
Soil	Depth	Mean soil depth (cm)
	pH	Mean soil pH
	SOM	Mean soil organic matter (% loss on ignition)
Landform	Slope	Mean surface slope
	Aspect	Mean surface aspect

affected the distribution of each species' demographic classes broadly following Wason and Dovciak (2017). We built linear mixed models for each demographic class with species importance as the response variable and mountain as a random effect using the lme4 package in r. The variance explained by fixed effects (climate, soil, and landform variables) in our full models (marginal R^2) was compared to a reduced model (one without either climate, soil, or landform variables) using likelihood ratio tests. We report significant coefficients for individual predictor variables from the best performing models (full vs. reduced models). Lastly, we compared the strength of the climate, soils and landform effects (the broad predictor categories) in terms of variance explained for each individual species and demographic class using ANOVA. Tukey's honestly significant difference (HSD) posthoc test was used to determine significant differences between the overall effects of the climate, soils, and landform. All statistical analyses were conducted using the R statistical language (R Development Core Team, 2019).

3 | RESULTS

3.1 | Overall demographic elevation mismatches

Elevation mismatches of seedlings and saplings relative to adult conspecifics indicated upslope shifts of seedlings relative to both adults and saplings for both conifer species (in agreement with hypothesis H1), but not for the two deciduous species (Figure 2). In agreement with H1, red spruce and balsam fir seedling distributions were shifted upslope of conspecific adult distributions, in contrast to sapling distributions that were either downslope of (red spruce) or similar to (balsam fir) their respective conspecific adult distributions (Figure 2). In contrast to conifer seedling distributions (and at odds with H1), deciduous seedlings were shifted downslope of their conspecific adults either corroborating (sugar maple) or contrasting (American beech) the distributions of the conspecific saplings relative to adults (Figure 2).

3.2 | Demographic elevation mismatches in gap and non- gap environments

Elevation mismatches between seedlings and conspecific adults differed for seedlings in gaps and seedlings under forest canopies (non- gap seedlings), and different patterns of seedling elevation mismatch emerged for coniferous and deciduous species. In agreement with hypothesis H2, red spruce and balsam fir seedling distributions were shifted upslope of conspecific adult distributions more so in gaps than under forest canopies (Figure 3). In contrast to H2, American beech and sugar maple seedling distributions relative to conspecific adults did not differ between gap and non- gap environments (Figure 3) as both gap and non- gap seedlings of both species were shifted downslope equally relative to conspecific adults (cf. Figure 2). Consistent with the greater upslope shifts of conifer seedling distributions in gaps (Figure 3), species importance of both red spruce and balsam fir increased significantly with canopy openness (Figure 4a) while canopy openness increased with elevation (Figures 4b). In contrast, species importance of sugar maple and American beech seedlings had no relationship to canopy openness (not shown). However, canopy openness tended to be lower at low elevations (where deciduous species were dominant) than at high elevations (where conifers tended to dominate; cf. Figure 4b).

3.3 | Environmental drivers of species spatial distributions and demography

In contrast to our hypothesis H3, climate variables were equally important in explaining the distributions of all three demographic classes (~15% to 20% of total variance explained on average) and climate was generally more important than landform or soil variables when all species were pooled together (Figure 5). However, soil variables explained somewhat larger proportion of total variance for seedlings than for saplings and adults (7.0% vs. 3.3% and 3.8%, respectively; Figure 5). Individual models for each species confirmed that climate variables were consistently significant and explained large and similar proportions of variance (~15%– 20%) for all size classes and species, except for American beech in which climate explained similar amount of variance for seedlings, but considerably less (~10%) for saplings or adults (Figure 6). Landform generally explained only a small proportion of variance (mostly <5%, ~6%– 9% for red spruce demographic classes and sugar maple adults; Figure 6). In contrast, compared to the distributions of adults and saplings, soils explained much more variance in the distributions of seedlings for three out of four species (sugar maple: 17.2%, balsam fir: 10.6%, American beech: 7.0%; Figure 6). Significance levels and coefficients for individual variables (see Table 2) for all the best performing models are in Table S1.

4 | DISCUSSION

4.1 | Seedlings as early indicators of tree species range shifts

The observation that tree seedling distributions along elevational gradients in our study were not coincident with the distributions of conspecific adult trees for any of the four main species potentially suggests early stages of ongoing species ranges shifts along the elevation gradient (cf. O'Sullivan et al., 2021; Pucko et al., 2011; Wason & Dovciak, 2017). However, our results did not provide clear evidence of ongoing upslope shifts for all species; instead, they further corroborate previous theory and studies that suggest range shifts are likely to continue to be individualistic (species- specific), and that range- shift variability within species is also possible (cf. Gleason, 1926; O'Sullivan et al., 2021; Wason & Dovciak, 2017). Importantly, our results did not support the idea that low- elevation deciduous tree species (sugar maple, American beech) were migrating upslope with warming climate. Instead, deciduous seedling distributions in our study suggested relatively

lower recruitment near the upper range margins, consistent with a potential ongoing downslope shift in these temperate deciduous species (in variance with our hypothesis H1; possible mechanisms discussed in *Environmental drivers of seedling distributions*). In contrast, seedling distributions of conifers (red spruce, balsam fir) suggested relatively greater recruitment near their upper range margins consistent with an ongoing upslope shift in species distribution (thus partially supporting H1) in agreement with predictions of spruce- fir forest range shift upslope and northward under future climate warming (Beckage et al., 2008; Cogbill & White, 1991). The resulting limited recruitment of all dominant tree species at the ecotone (transition) between low- elevation deciduous and high- elevation conifer forests is surprising (given the expected upslope shifts of low elevation species), and it may potentially lead to a novel tree species composition at the ecotone (see Figure S5) rather than to a gradual synchronous upslope move of the current

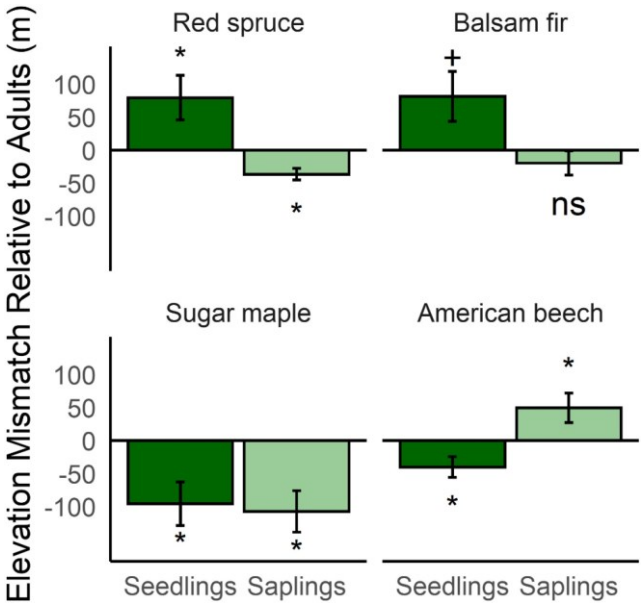

FIGURE 2 Mean elevation mismatch (± standard error) of seedling and sapling distributions relative to conspecific adult distributions of four common tree species in Northeastern United States. Positive values indicate upslope shifts, and negative values indicate downslope shifts, of seedling or sapling distributions relative to conspecific adult distributions. The statistical significance of elevation mismatches is reported above bars as follows: *($P < 0.05$), +($P < 0.1$), ns (not significant). Elevation mismatches were calculated from logistic regressions characterizing the probability of occurrence of species demographic classes (seedlings, saplings, and adults) over elevation.

forest communities suggested by some earlier theories (Breshears et al., 2008; Williams & Jackson, 2007).

Importantly, our findings are consistent with the idea that seedling distributions reflect more recent climatic trends than do sapling distributions. While seedling distributions of high- elevation, relatively cold-tolerant conifers (red spruce, balsam fir) were shifted upslope of conspecific adults (consistent with upslope migration due to climate warming), conifer sapling distributions were shifted downslope (red spruce) or had a similar distribution (balsam fir) relative to conspecific adults, as noted in our previous work in this system (cf. Wason & Dovciak, 2017). Since our study species are all shade- tolerant and have relatively slow growth rates, these saplings are generally older than seedlings. Therefore, sapling distributions may reflect a more historical climate than the younger seedlings. For example, most of the seedlings in our surveys were likely established during the last two decades, which were the hottest on record (NOAA National Centers for Environmental Information, 2022). Indeed, based on ring counts of >700 seedlings collected (<0.5 m tall) from the field from our study tree species, >95% of collected individuals were likely less than 20 years old (Tourville, unpublished data). Given that the seedling niche is generally narrower, and seedling mortality generally higher than sapling or adult niche breadth and mortality (Grubb, 1977; Leck et al., 2008), seedling distributions have two important properties to consider in the context of

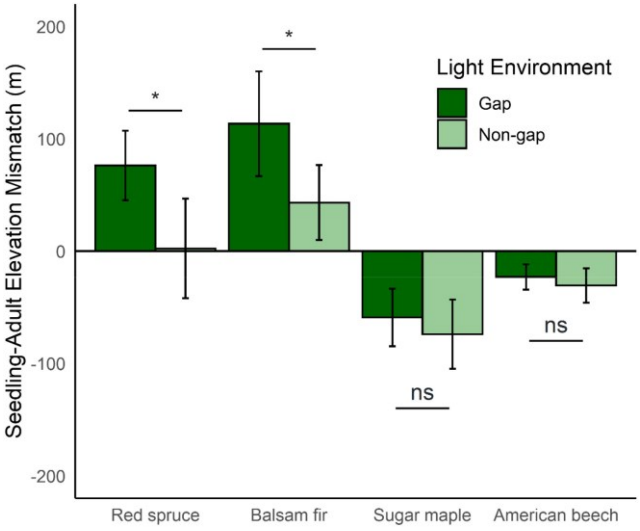

FIGURE 3 Estimated elevation mismatch (mean and standard error) relative to adults for conspecific seedlings from both gap and non- gap environments based on logistic regressions for probability of occurrence from species relative frequencies. Significance values from one- sample t-tests to test if mismatch estimates between the two seedling groups (gap vs. non- gap) were significantly different from each other are reported above each bar (*$p < 0.05$, ns = not significant).

changing climatic conditions: while (i) seedling distributions can be more responsive to recent climatic trends and serve as their early indicators, (ii) mortality at the seedling life stage may reshape the distribution of future saplings and adults. For example, specific biotic interactions (e.g. limited mycorrhizal colonization, herbivory, disease) can potentially affect seedlings more than saplings or adult trees (which have a greater capacity to handle these stressors), and thus they can greatly constrain seedling responses to climate (Brown & Vellend, 2014; Carteron et al., 2020; HilleRisLambers et al., 2013; Lafleur et al., 2010; Leck et al., 2008; Urli et al., 2016).

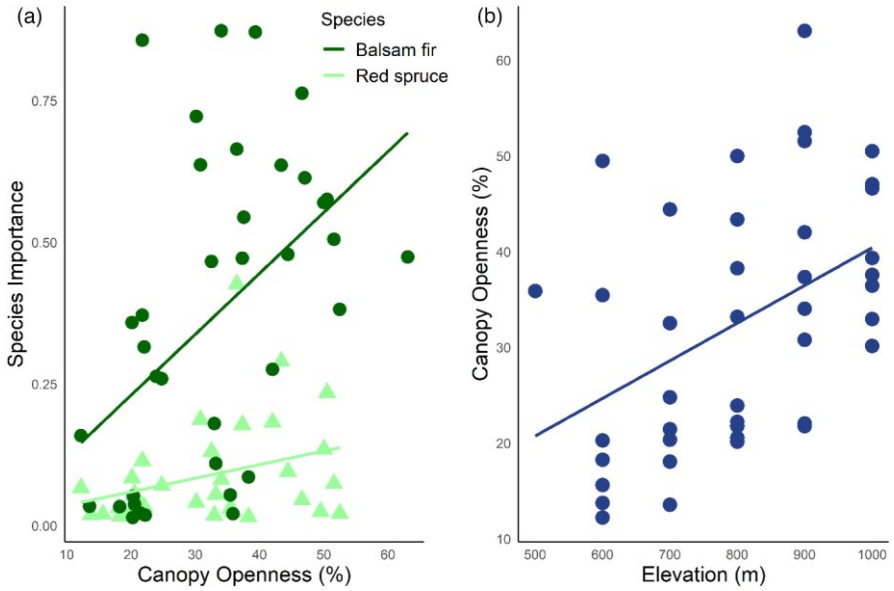

FIGURE 4 The relationship of seedling species importance value relative to canopy openness for conifers (a) and changes in canopy openness with elevation (b). In (a) seedling species importance values per site (elevation) and linear fits are shown relative to elevation for balsam fir (dark green filled circles and line; $p = 0.003$, $R^2 = 0.23$) and red spruce (light green filled triangles and line; $p = 0.07$, $R^2 = 0.1$). Seedling species importance values and fits are not shown for deciduous species to preserve clarity since they were unrelated to canopy openness. In (b) canopy openness is shown to increase with elevation ($p < 0.001$, $R^2 = 0.21$). Species importance values were derived from averaging site level relative frequency and relative density (gap and non-gap combined).

4.2 | Role of forest gaps in ecotone dynamics

Our results suggest that forest gaps may serve a critical role in facilitating shifts in conifer seedling distributions from lower to higher elevations, although gaps did not affect elevational distributions of deciduous seedlings (thus only partially supporting hypothesis H2). While the role of canopy gaps in forest stand development and succession in mesic forests under moderate wind disturbance is well known (Runkle, 1981; Runkle, 1982; Sprugel, 1984), the role of gaps has not yet been fully considered in the context of climate- induced tree species migrations and range shifts across ecotones. While most studies of climate- induced tree species ranges focus on broad- scale drivers of forest change (e.g. Boisvert- Marsh & Blois, 2021; Iverson et al., 2008; Liang et al., 2018), our results suggest that forest gaps at local scales may play important roles in facilitating tree species range shifts (at least in some conditions and for some species). Thus, forest gaps have the potential to serve a role in monitoring climate- induced changes in tree populations in order to detect early stages of tree species migrations. However, the role of forest gaps is not absolute.

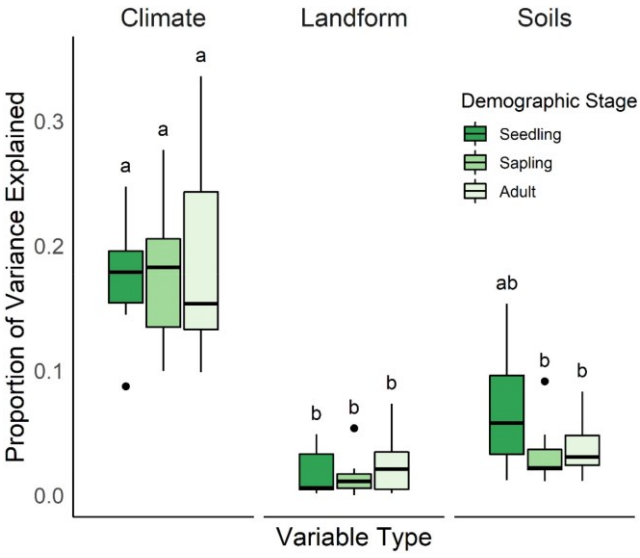

FIGURE 5 The proportion of variance explained by multiple climate, landform, and soil variables (see Table 2) in the models of the distributions of demographic classes (seedlings, saplings, and adults) for the four dominant tree species in Northeastern United States (American beech, sugar maple, red spruce, and balsam fir) combined. Species distributions were modelled as species importance values (iv) integrating species relative frequency and density. Statistically significant differences were determined using Tukey's HSD tests (alpha = 0.05) and indicated by different letters. Boxplots display median values with 25% quantiles.

For example, gaps did not seem to play any role in our study in elevational distributions of seedlings of the two deciduous species, likely because both sugar maple and American beech are quite shade tolerant (Canham et al., 1994; Kobe et al., 1995) and because forest gaps at low elevations were less open and thus more light- limited than high- elevation gaps in spruce- fir forests. The pattern of increasing canopy openness with elevation is likely due to both differences in crown architecture of deciduous (spreading forms) versus conifer (narrow conical forms) trees, as well as the increased intensity and frequency of wind disturbance events at exposed high elevations compared to low elevations (Boucher & Grondin, 2012; Pelt & Franklin, 2000).

4.3 | Environmental drivers of seedling distributions

Our results suggest that climate explained the most variation in species elevational distributions for all dominant species and demographic classes in a similar way (in contrast to hypothesis H3). Plant species distributions are constrained by both physiological limits imposed by climate and by competition from other plant species (Post, 2013; Reich et al., 2015). Deciduous temperate species (e.g. American beech, sugar maple) tend to be limited to lower elevations by climate and competition from cold-adapted species at cooler high- elevation environments, but experimental warming has been shown to alleviate such limits (cf. Reich et al., 2015; Sendall et al., 2015). Conversely, balsam fir is confined to cold and wet areas typical of high elevations (Cogbill & White, 1991), while red spruce is ubiquitous across the elevation gradient, but its range limits can be negatively affected by warming and air pollution (Koo et al., 2014). Rising temperatures and changes in precipitation have likely alleviated the fundamental constraints on temperate deciduous (northern hardwood) trees from migrating upslope; however, other limiting drivers, such as specific land- use legacies (i.e. regional historic logging), edaphic, and biotic factors, have been suggested to mask or inhibit upslope shifts (Brown & Vellend, 2014; Carteron et al., 2020; Fisichelli et al., 2012; HilleRisLambers et al., 2013; Lafleur et al., 2010; Wason & Dovciak, 2017). For example, low pH as a result of base cation leaching, herbivory, and lack of suitable mycorrhizal fungal mutualists may limit sugar maple recruitment, while disease (beech bark disease) may inhibit beech survival and recruitment (Carteron et al., 2020; Fisichelli et al., 2012; Frerker et al., 2013; Halman et al., 2015; Horsley et al., 2000; Sullivan et al., 2013). We posit that a better understanding of land- use legacies, edaphic, and biotic factors can help explain downslope shifts of some tree species across various montane systems (Lenoir et al., 2010; Wason & Dovciak, 2017).

5 | CONCLUSIONS

High- elevation montane conifer forests harbour endemic species and provide important ecological services such as carbon storage and the protection of fragile spodosols (Siccama, 1974; White & Cogbill, 1992). The extreme environment in which these montane forests occur makes them vulnerable to climate change and other global change drivers, such as air pollution and acid deposition (Alexander et al., 2018; Klanderud et al., 2015; Koo et al., 2014). Our study demonstrates the importance of monitoring both tree seedling banks and forest gaps in assessing changes in forest composition and species ranges under a changing climate. We acknowledge that differences in the distributions of various tree life stages could be influenced by ontogenetic niche shifts, as high mortality of seedlings could alter the perceived range shifts in our system (Álvarez- Yépiz et al., 2014; Bertrand et al., 2011; Ni & Vellend, 2021; O'Sullivan et al., 2021; Werner & Gilliam, 1984). However, given the limited long- term historical data on tree distributions along elevation gradients and the requirement that seedling recruitment be occurring at the leading edge of a range shift, the data we report here still provides important information on the availability of seedlings and the potential for a longer- term range shift. Seedlings respond to contemporary climate; thus, monitoring seedling distributions provides researchers with a valuable first look into possible future trajectories of species distributions and forest composition. Incorporating processes of seedling recruitment and seedling surveys within multiple parts of a species range as well as forest canopy gaps into monitoring systems is currently rare,

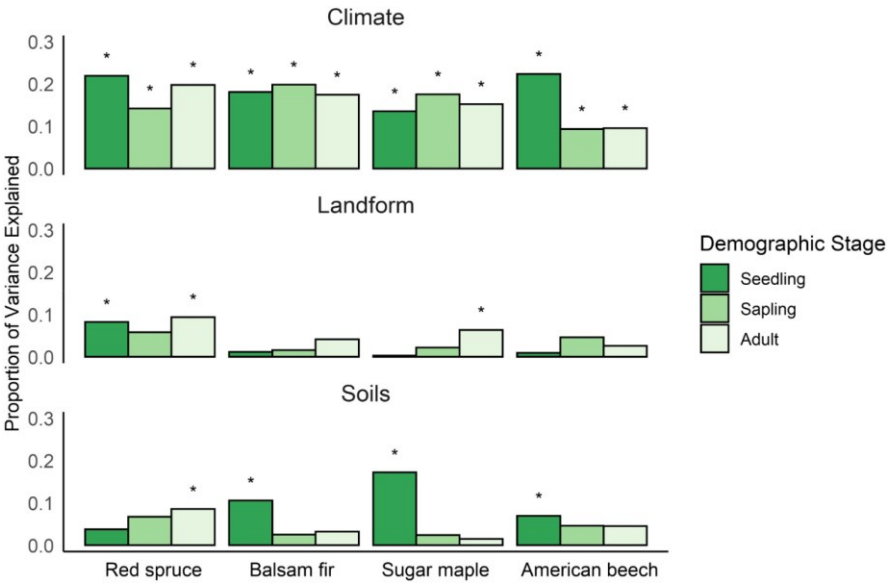

FIGURE 6 The proportion of variance explained by multiple climate, landform and soil variables (see Table 2) in the models of the distributions of demographic classes (seedlings, saplings and adults) for the four dominant tree species in Northeastern United States (American beech, sugar maple, red spruce and balsam fir), displayed individually. Species distributions were modelled as species importance values (iv) integrating species relative frequency and density. Statistically significant differences were determined using Tukey's HSD tests (alpha = 0.05) and indicated by different letters.

but doing so should improve an understanding of forest transitions at local scales, particularly across environmental gradients (Copenhaver- Parry et al., 2020; De Pauw et al., 2022; Zhang et al., 2022).

The observed lag between tree species migration and climate change velocities implies that future tree distributions are not predictable by examining climate in isolation (Liang et al., 2018; Sittaro et al., 2017). Biotic interactions and ecological processes at local scales affect our ability to forecast the compositional changes in future forests. Disturbances which create forest gaps promotes seedling recruitment and accelerates forest regeneration and species turnover, as is the case with high- elevation spruce- fir forests in the northeast (cf. Brice et al., 2020). Thus, evaluating non- climatic factors together with the effects of gap- phase dynamics across ecotones and along environmental gradients is critical for our understanding of climate- induced species range shifts in forest communities.

AUTHOR CONTRIBUTIONS

Jordon C. Tourville, Jay W. Wason, and Martin Dovciak conceived the ideas and methodology for this study; Jordon C. Tourville analysed the data and wrote the manuscript with substantial input from Jay W. Wason and Martin Dovciak; data were collected by Jordon C. Tourville and Jay W. Wason, and all authors contributed to editing manuscript drafts and all gave final approval for publication.

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CONFLICT OF INTEREST

None declared.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All demographic and environmental data and R code used in this publication will be freely available in the DRYAD data repository https://doi.org/10.5061/dryad.qz612 jmh6 (Tourville, 2022).

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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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