

Relationships between juvenile tree survival and tree density, shrub cover and temperature vary by size class based on ratios of abundance

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Abstract

Global change drivers are altering forest dynamics, yet how these factors influence tree survival across early developmental stages (i.e., seedling to recruited sapling) over large geographies is not well understood. We developed a novel approach to evaluate controls on seedling and sapling survival. This approach was demonstrated on a set of systematic forest inventory plots across the northeastern USA in which seedlings were tallied within six height classes, allowing for a detailed assessment of the stages at which demographic bottlenecks in juvenile tree development are often observed. Forest inventory subplots containing a study species were divided into overlapping bins along an environmental or ecological gradient, and ratios of abundance between successive size classes were used to infer relative survival rates. Relationships between 10 common tree species and tree density, shrub cover, and mean annual temperature were assessed. As seedling height class increased, we observed shifts from positive to negative associations with shrub cover and large tree density. Our results suggest that observed patterns of sapling and tree abundance may belie complex and sometimes opposing influences on seedling survival that are important to quantify when predicting and managing for successful tree recruitment and future canopy tree composition.

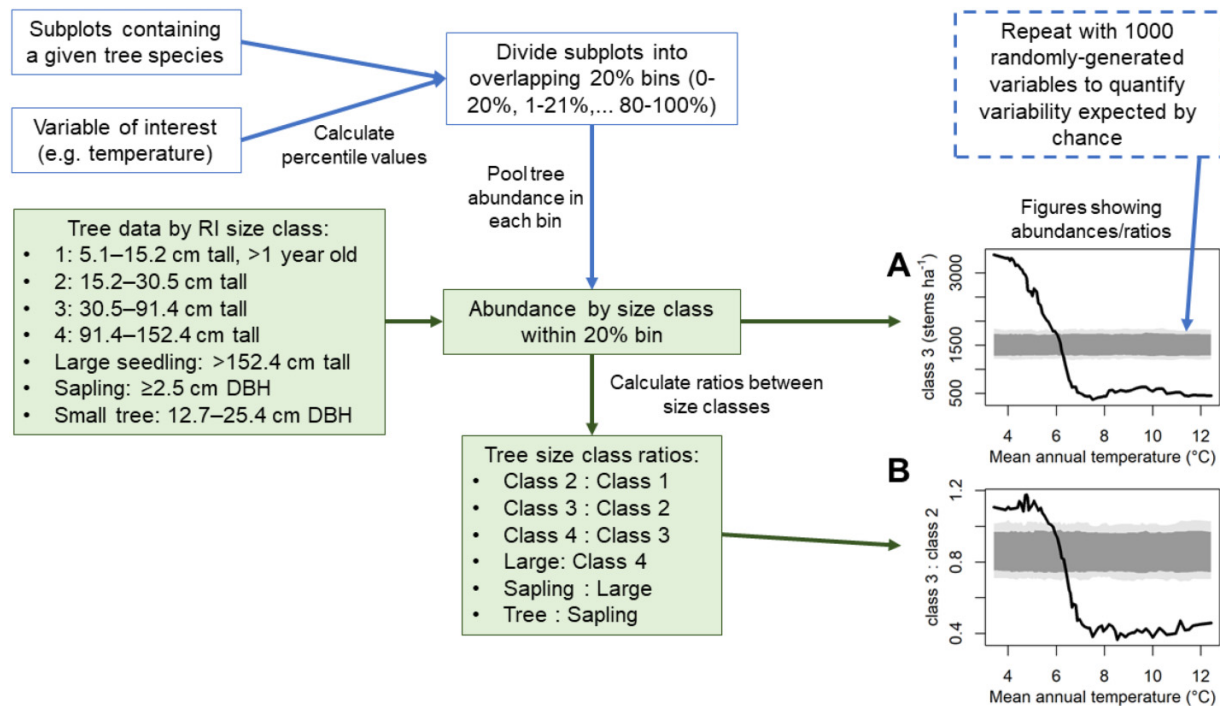
Key words: tree regeneration, regeneration survival, regeneration size, forest inventory, northeastern USA

Introduction

Forecasting changes in abundance and composition of tree species is increasingly important in the context of global change drivers such as climate change, shifting disturbance regimes, and the spread of invasive species (McDowell et al. 2020). Ecologists and foresters have long recognized that juvenile trees (i.e., seedlings and saplings) tend to have a narrower range of environmental tolerance than adult trees; therefore, the stand initiation and understory re-initiation stages of stand development (cf. Oliver and Larson 1996) are crucial to shaping forest composition and function (Mason 1936; Grubb 1977; Seidl and Turner 2022). Studies comparing the environmental niche of juvenile and adult trees have provided insight into this difference in environmental tolerance as well as potential evidence for ongoing range shifts (Bell et al. 2014; Dobrowski et al. 2015; Serra-Diaz et al. 2016). In addition, recent work highlights how the response of tree demography to climate change varies by life stage, which can either amplify or buffer climate-driven shifts in tree species abundance (Sharma et al. 2022; Yang et al. 2022). Therefore, the environmental drivers of demographic rates (e.g., growth, recruitment, and mortality) may be more effective to study than presence or abundance when seeking to forecast forest dynamics (Schultz et al. 2022).

Ideally, tree survival and recruitment are quantified using plots in which individual stems are identified and tracked over time. Regional to national-scale forest inventory programs, such as the United States Department of Agriculture (USDA) Forest Service Forest Inventory and Analysis (FIA) program (Bechtold and Patterson 2005), track individual saplings and trees in repeated plot measurements and therefore offer the opportunity to directly assess sapling and tree recruitment rates and their underlying influences over broad scales (Zhu et al. 2015; Harris et al. 2022). Yet, individual seedlings are not typically tracked in forest inventories because it is time- and resource-intensive. Therefore, direct studies of seedling survival and growth are limited to fine scales (George and Bazzaz 1999; Meiners and Martinovic 2002; Beckage and Clark 2003; Walters et al. 2016). As a result, a great need remains for the development of approaches that enable broad-scale assessments within the seedling stage to forecast near-term stand development and indicate how global change drivers may affect forest composition and structure. Analysis across seedling size classes may be particularly useful to help identify whether and where demographic bottlenecks in development occur, for example whether smaller seedlings are more climate-sensitive (Clark and D'Amato 2023) or whether relationships with understory

Fig. 1. Proposed methodology for using tree regeneration tallies by size class from forest inventory data (regeneration indicator (RI) subplots) to examine the effect of a given variable on (a) abundance by size class and (b) relative survival rates based on ratios between size classes. Solid black lines in (a) and (b) represent abundance/abundance ratio values within each 20% bin (in this case based on percentiles of mean annual temperature) plotted across the range of values for a given variable.



vegetation shift from facilitative to competitive as seedlings mature (Callaway and Walker 1997; Legras et al. 2010; Walters et al. 2020).

One way to identify potential influences on juvenile tree survival in the absence of tagged and remeasured stems is to calculate ratios of abundance between size classes along key gradients of interest such as mean annual temperature. However, within any single field plot or small group of plots, relationships are likely to be obscured by effects of forest developmental stage or other stand- and site-level factors. The potential large-scale monitoring issues of noise and bias present substantial obstacles when trying to leverage abundance data to examine influences on tree survival over different developmental stages. To overcome these obstacles, we propose grouping inventory subplots into large bins that are likely to represent a broad spectrum of stand- and site-level conditions ($n \geq 250$ subplots per bin) and using ratios of abundance between size classes within these bins as indices of relative survival rates.

Our work utilizes the FIA Regeneration Indicator (RI) dataset, an emerging tree regeneration dataset that offers the ability to perform assessments within the tree seedling stage (McWilliams et al. 2015; Harris et al. 2022). Under RI protocols, a systematically sampled subset of FIA plots throughout the northeastern US is surveyed using more detailed tree regeneration protocols involving tallying tree seedlings by six height classes (Fig. 1) instead of the single size class traditionally used by the FIA program (i.e., ≥ 15.2 cm tall and < 2.5 cm diameter at breast height (DBH) for softwoods and ≥ 30.5 cm

tall and < 2.5 cm DBH for hardwoods). The RI dataset has previously been used to determine whether advance regeneration is adequate to restock stands based on expected mortality rates for different-sized seedlings drawn from the literature (Vickers et al. 2019) and to predict sapling recruitment in remeasured plots based on seedling abundance by size class (Harris et al. 2022). However, RI data have not been used to investigate drivers of juvenile tree abundance and survival through successive size classes as we do in this work.

Here, we propose and demonstrate a methodology for using tree regeneration survey data to quantify how individual factors relate to juvenile tree abundance and survival across different size classes. Large tree density (≥ 25.4 cm DBH), shrub cover, and mean annual temperature were considered as potential drivers (Fig. 1). In brief, this methodology involves dividing all forest inventory subplots containing a given species into overlapping bins along a gradient of a variable of interest. Next, mean abundance by size class is calculated within each bin as well as ratios of abundance between size classes as a proxy for survival. Finally, abundance and survival are plotted over confidence intervals (CIs) representing the range of values expected by chance alone to assess the shape and significance of each relationship.

In the process of demonstrating this methodology, we focused on the following research questions:

- 1) Do relationships between abundance and survival and large tree density, shrub cover, and mean annual temperature vary among size classes and common tree species?

Table 1. Number of subplot measurements in which each species was present ($n = 21532$ total) and mean (standard deviation) of density of large trees (>25.4 cm DBH), shrub cover, and mean annual temperature within those subplots.

Species	Subplots	Trees·ha ⁻¹	Shrub cover (%)	Mean temperature (°C)
<i>Abies balsamea</i>	4105	109 (120)	20.9 (24.2)	4.8 (1.3)
<i>Acer rubrum</i>	11 003	143 (125)	22.8 (25.7)	7.3 (2.8)
<i>Acer saccharum</i>	5888	147 (114)	16.3 (20.9)	7.2 (2.9)
<i>Betula alleghaniensis</i>	2595	143 (122)	14.8 (19.9)	5.5 (1.7)
<i>Fagus grandifolia</i>	3630	162 (120)	12.3 (18.3)	7.4 (2.6)
<i>Fraxinus americana</i>	5057	143 (113)	22.2 (23.9)	9.2 (2.8)
<i>Fraxinus nigra</i>	1334	112 (121)	26.8 (25.0)	5.1 (1.4)
<i>Ostrya virginiana</i>	2098	144 (110)	15.6 (19.2)	7.7 (2.8)
<i>Prunus serotina</i>	4901	146 (119)	26.3 (26.3)	8.9 (2.8)
<i>Picea rubens</i>	1847	130 (124)	14.3 (20.0)	5.0 (1.4)

- 2) Does investigating relative differences in juvenile tree survival using abundance ratios reveal relationships that are not apparent when only investigating abundance?

Methods

The FIA program is a systematic national forest inventory in which forest land is divided into 24 km² hexagons with one permanent field plot each (Bechtold and Patterson 2005). Each FIA plot contains four circular subplots of 168 m² in which adult trees (>12.7 cm DBH) are measured, with one subplot at the center and the others spaced 36.6 m from the center plot at 0°, 120°, and 240° directions. Nested 13.5 m² microplots within each subplot are used to collect data on tree seedlings and saplings (2.5–12.6 cm DBH). Beginning in 2012, the RI protocols with six seedling height classes tallied within each microplot were implemented over 12.5% of FIA plots across the 24 states of the northeastern and midwestern USA falling within the region of the USDA Forest Service Northern Research Station (McWilliams et al. 2015).

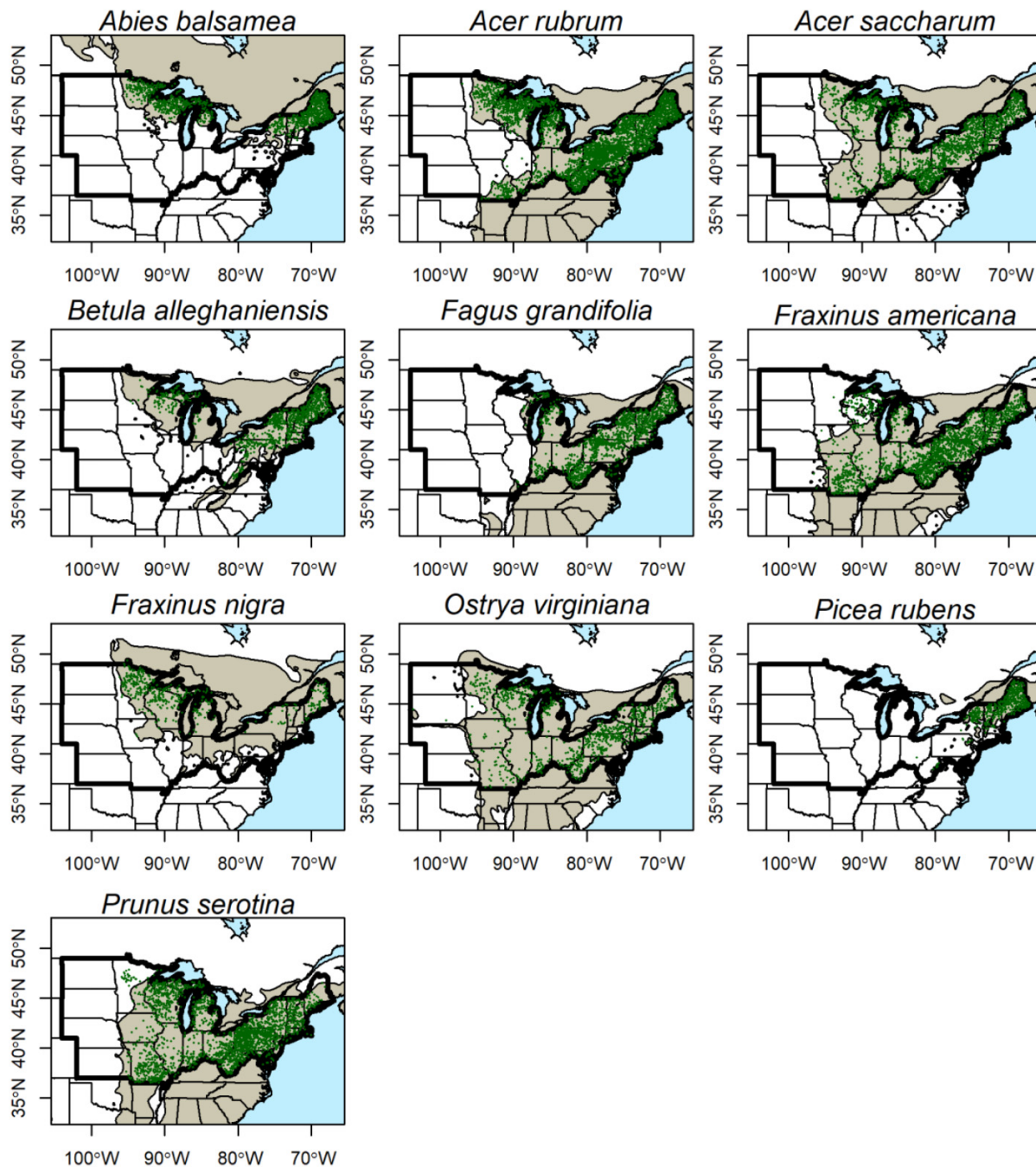
We extracted abundance by tree species and size class at the subplot level for all RI plot measurements, accessed from the FIA database on 9 February 2023. RI plots are remeasured at 5–7-year intervals, and for the purposes of this analysis remeasured subplots were treated as separate observations. Notably, these subplot remeasurements cannot be used to directly quantify seedling growth and mortality because individual seedlings are not tagged and tracked over time. Seven size classes were used for analysis: the six seedling height classes with Classes 5 and 6 seedlings (1.52–3.05 m and ≥ 3.05 m tall, respectively) combined, saplings, and small trees (12.7–25.4 cm DBH). Classes 5 and 6 seedlings (hereafter “large seedlings”) were combined because some tree species commonly attain 2.5 cm DBH before reaching 3.05 m tall, meaning that Class 6 seedlings are rare for these species and therefore that the ratio of saplings to Class 6 seedlings may be an unreliable indicator of survival from large seedling to sapling size.

For analysis, we selected the tree species for which each of these seven size classes was present in ≥ 300 subplots. This

size-class specific threshold was used rather than the overall number of subplots in which each species was present (Table 1) because analyses were performed by size class; therefore, we wanted to ensure an adequate sample size within each class. The following relatively common 10 species across the study region were selected: balsam fir (*Abies balsamea* L.), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britton), beech (*Fagus grandifolia* Ehrh.), white ash (*Fraxinus americana* L.), black ash (*Fraxinus nigra* Marsh.), hophornbeam (*Ostrya virginiana* (Mill.) K. Koch), red spruce (*Picea rubens* Sarg.), and black cherry (*Prunus serotina* Ehrh.). These species represent a range of habitat preferences and functional traits, although the list is skewed toward late-successional and shade-tolerant species. Four of these species have most of their range contained in the study area (*Acer saccharum*, *B. alleghaniensis*, *Fraxinus nigra*, and *Picea rubens*), one is a northern species reaching its southern range limit within the study area (*Abies balsamea*), and the remaining five species have ranges extending well south of the study area (Fig. 2).

We considered three potential drivers of tree abundance and survival to demonstrate our methodology: large tree density, shrub cover, and mean annual temperature. These variables were chosen because they represent different categories of drivers: overstory vegetation, understory vegetation, and climate. Large tree density, or the total density (stems·ha⁻¹) of trees ≥ 25.4 cm DBH within each subplot, is a proxy for forest successional stage, overstory canopy, and light availability. Shrub cover is a proxy for biotic interactions with shrubs, which may compete with tree seedlings or facilitate them by influencing microclimate or herbivory (Callaway and Walker 1997; Walters et al. 2016). The FIA program visually estimates shrub cover to the nearest 1% within each condition in a subplot, with “condition” being defined as an area with the same land use and relatively homogenous forest characteristics (Bechtold and Patterson 2005). In the case of more than one condition being present within a subplot, the condition class at the center of the microplot was used to extract shrub cover to select the condition most relevant to the seedling and sapling tallies. Mean annual temperature from 1991 to 2020 from the Parameter-elevation Regressions on

Fig. 2. Regeneration indicator field plots in which each species was present (green dots) within the study region (heavy black line) as well as the range of each species (shaded region). Figures were created using R version 4.2.3 and assembled from publicly available data: the Forest Inventory and Analysis database (<https://apps.fs.usda.gov/fia/datamart/datamart.html>), state boundaries (<https://www.census.gov/geographies/mapping-files.html>), and species ranges (Little 1971, <https://web.archive.org/web/20170127093428/https://gec.cr.usgs.gov/data/little/>).



Independent Slopes Model (PRISM) dataset (Daly et al. 2008) was extracted to RI plot locations. Because the PRISM dataset consists of 4 km grid cells and because FIA plot locations are perturbed and/or swapped with nearby plots having similar characteristics (Burrill et al. 2021), this temperature variable represented mesoscale climate in the neighborhood of each plot rather than local climate as affected by terrain. Also, it should be noted that as a plot-level variable, temperature had

a smaller effective sample size than the two other variables that were at the subplot level.

Estimating response of abundance and survival

For a given species, subplots containing a live individual of any size were retained (including seedlings, saplings, and trees of any size) to restrict the analysis to subplots in which the species was currently present (Table 1). The analysis of

abundance and size class ratios proceeded as follows (summarized in Fig. 1):

First, percentile values for the three independent variables were used to divide subplots containing the species of interest ($n = 1334\text{--}11\,003$ subplots, Table 1) into overlapping 20% bins, e.g., 0–20th-percentile shrub cover, 1–21st-percentile shrub cover, etc. Each of these bins contained 250–2112 subplots depending on the species being analyzed. Note that this use of percentile bins also meant that sample size was the same across each environmental gradient within a given species. Using these broad bins was a key step to reduce potentially confounding stand- and site-level influences. For example, a closed-canopy stand with limited opportunity for recruitment would be expected to contain relatively few seedlings >1.5 m tall, whereas a stand regrowing after a recent disturbance might feature high abundance of large-sized seedlings and saplings. Once subplots are divided into overlapping bins, however, each bin will typically contain a fuller spectrum of stand- and site-level conditions, and species abundance within these bins will be more reflective of broader demographics. We found that using 20% bins resulted in smoother and more ecologically plausible relationships than smaller bins for our given range of sample sizes (examples using 10% bins are shown in Figs. S21 and S22).

Secondly, mean abundance by size class was calculated within each bin. From these mean abundance values, the ratio between each pair of successive size classes was then calculated as a proxy for relative survival and successful recruitment to the next size class. For example, a higher ratio of Class 2 to Class 1 seedlings suggests, in the absence of other confounding factors, that a greater proportion of Class 1 seedlings are attaining Class 2 size. The resulting mean abundances and ratios were visualized by plotting them against the median value of the independent variable for each bin (e.g., heavy black lines in panels A and B of Fig. 1).

Thirdly, to separate non-significant relationships from relationships of potential ecological significance, we quantified the range of values for abundance or abundance ratios that would be expected due to chance alone. We used a simulation-based approach in which the subplots containing a given species were again divided up into 20% bins, with abundance and ratios of abundance calculated as before but using random-number variables instead of one of the three independent variables. For each species, we ran 1000 simulations and used the resulting abundance and abundance ratio values to construct 95% and 99% CIs representing the range of values expected due to chance (e.g., dark and light gray regions in panels A and B of Fig. 1). Observed relationships lying partly beyond the 95% CI and especially the 99% CI may be considered significant in that they are unlikely due to chance, although it should be noted that our methodology is limited to identifying empirical associations rather than the mechanisms underpinning such associations.

Trends across species and size classes

After using our methodology to produce figures showing the relationships between each species and each independent variable by tree size class, major findings were summarized

by aggregating results across (1) species and (2) size class. To aggregate results, we manually classified the shape of each relationship as positive (increasing), negative (decreasing), unimodal, or other (Tables S1 and S2). For the purposes of this aggregated analysis, we only considered relationships in which >5% of values lay beyond the 99% CI as significant and did not classify the shape of non-significant relationships. The 5% threshold and use of the 99% CI were chosen to be conservative in our identification of potentially significant relationships. We then tallied the number of species within each size class exhibiting each type of relationship to identify major trends by size class across species. Finally, we identified the type(s) of relationship present within each species–variable combination to indicate the extent to which intra-specific relationships were consistent across size classes. For this latter comparison across size classes, we omitted the small tree class and the small tree to sapling ratios to focus on juvenile trees. Although we focus our analysis and discussion on high-level trends, the full set of results for individual species is shown in Supplementary Figs. S1–S20.

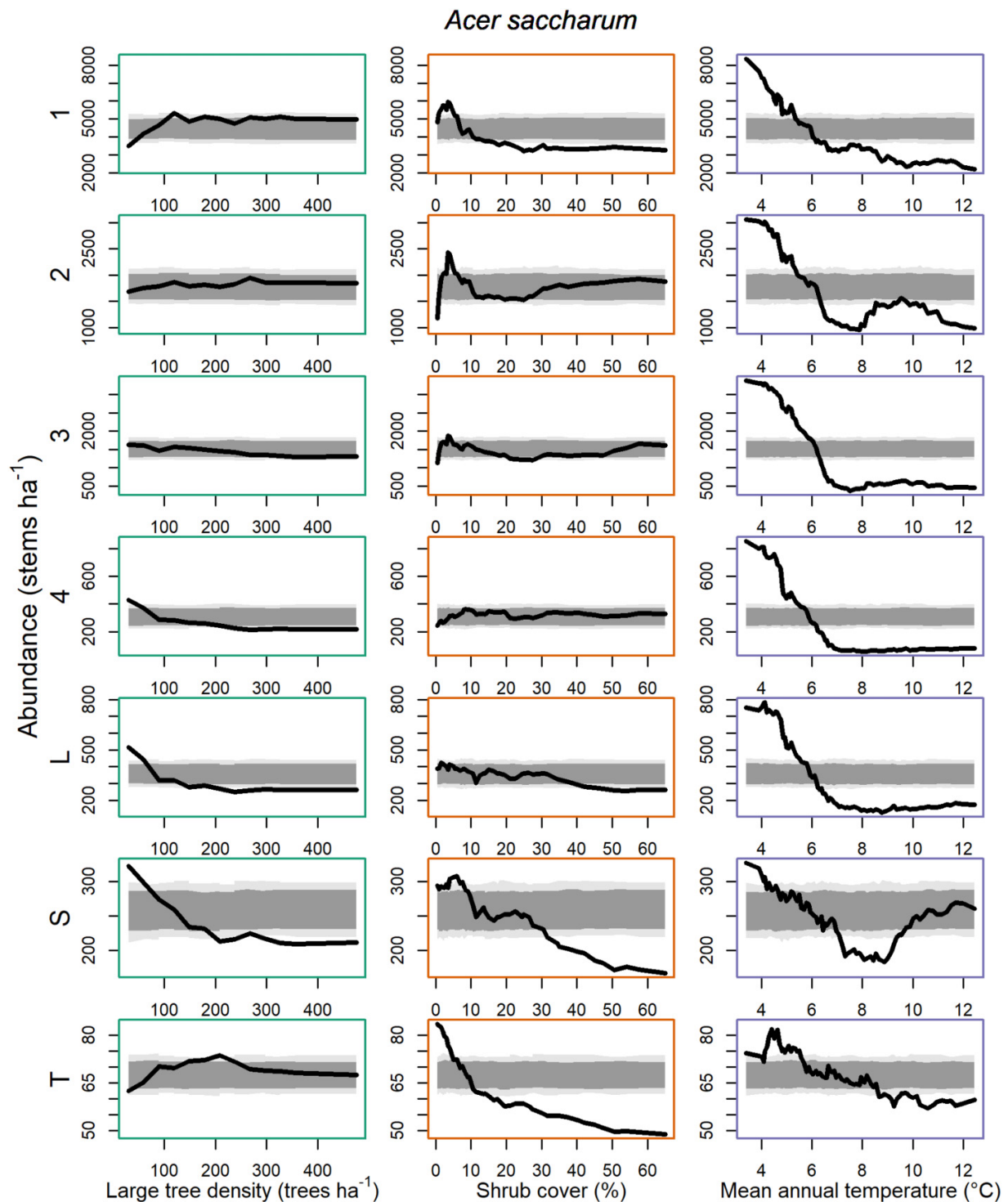
Results

Applying our methodology to the 10 tree species and 3 independent variables revealed a diversity of relationships across size classes and species. Here, we show results for *Acer saccharum* as an example before presenting high-level trends across size classes and species. The relationship between abundance of *Acer saccharum* and large tree density switched from a positive relationship for the smallest seedlings (Class 1) to negative relationships for Class 4 seedlings to saplings to a unimodal relationship for small trees (Fig. 3). This switch was generated by a negative association between large tree density and survival from Class 3 to 4, countered by a positive association with the ratio of small trees to saplings (Fig. 4). For shrub cover, relationships with abundance switched from negative for Class 1 seedlings to mixed or non-significant relationships for Classes 2–4 and then reverted to negative relationships for large seedlings through small trees. An examination of abundance ratios and shrub cover showed that survival from Class 1 to 2 was twice as high under high shrub cover (~60%) than near-zero shrub cover, yet the relationship between shrub cover and survival from Class 4 to large seedling size was negative. Relationships between *Acer saccharum* abundance and temperature were negative for all but the sapling class (Fig. 3), yet this belied highly variable relationships between temperature and survival (Fig. 4). Temperature had a strongly negative relationship with survival from Class 2 to 3 yet strongly positive relationships from Class 4 to large seedlings and from large seedlings to saplings.

Trends across species

When relationships were tallied by size class across species, some common trends were evident (Fig. 5). The percentage of non-significant relationships varied substantially from <10% for abundance–mean annual temperature relationships to >60% for survival–large tree density relationships. Relationships between Class 1 seedling abundance and large tree density were either positive (three species) or

Fig. 3. Abundance by size class (rows) for *Acer saccharum* along gradients of the three variables analyzed (columns). Dark (light) gray regions are 95% (99%) confidence intervals of values expected by chance. Size classes are seedling height Classes 1–4. L, large seedlings (Classes 5 and 6); S, saplings; T, small trees.

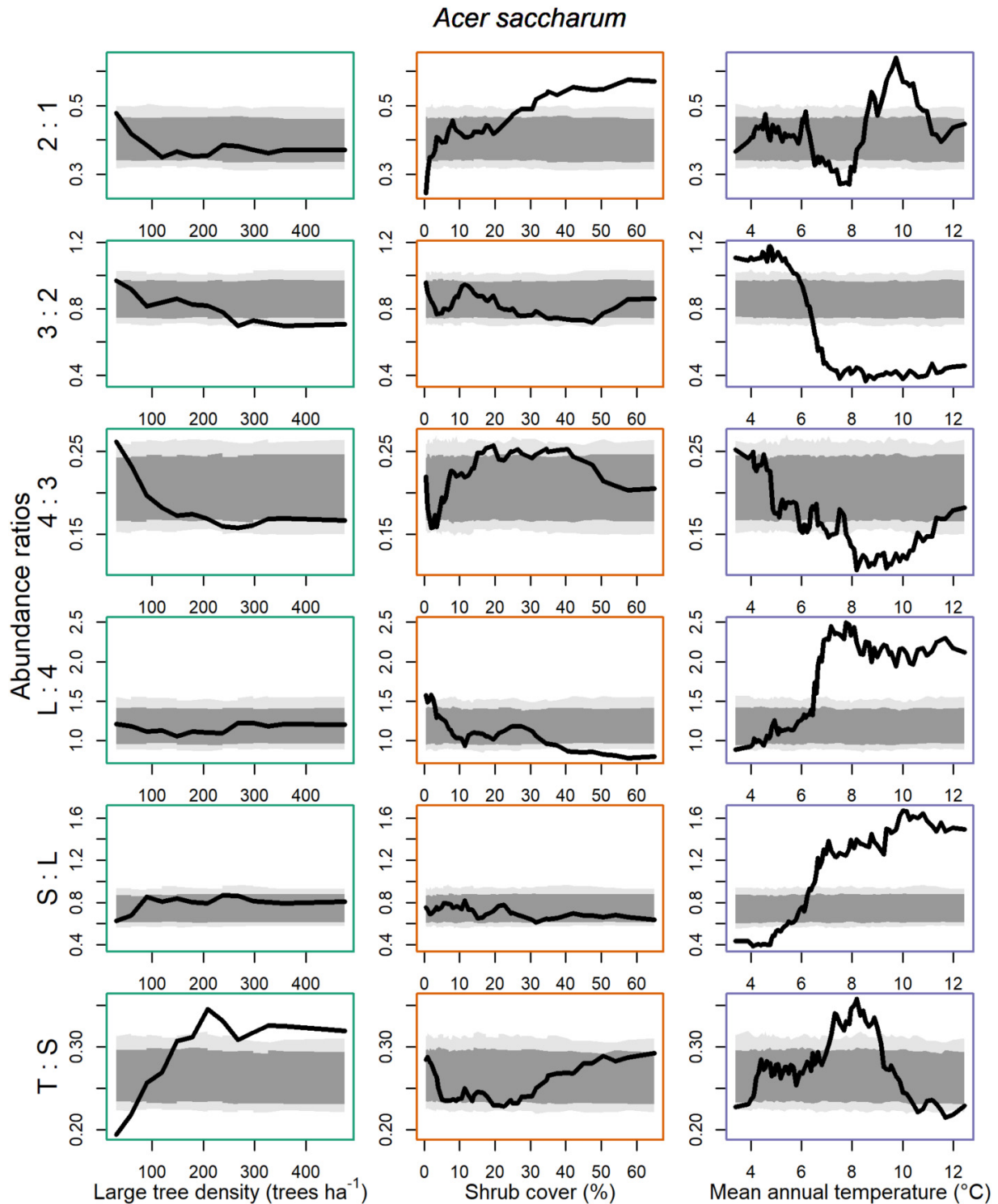


non-significant, but from Class 2 to sapling size, the number of negative relationships increased and 9 of 10 species were negatively related to large tree density for large seedlings and saplings. This shift was driven by negative relationships between seedling survival and large tree density especially at the Class 3 to 4 transition (seven negative relationships). Con-

versely, the ratio of small trees to saplings was positively related to large tree density for most species.

For shrub cover, positive relationships with abundance were most prevalent at Class 4 (six species) and negative relationships were most common at Class 1 and small tree size (Fig. 5). Between 1 and 4 unimodal relationships were

Fig. 4. Ratios of abundance between size classes (rows) for *Acer saccharum* along gradients of the three variables analyzed (columns). Higher ratios indicate relatively better survival between a given pair of size classes. Dark (light) gray regions are 95% (99%) confidence intervals of values expected by chance. Size classes are seedling height Classes 1–4. L, large seedlings (Classes 5 and 6); S, saplings; T, small trees.

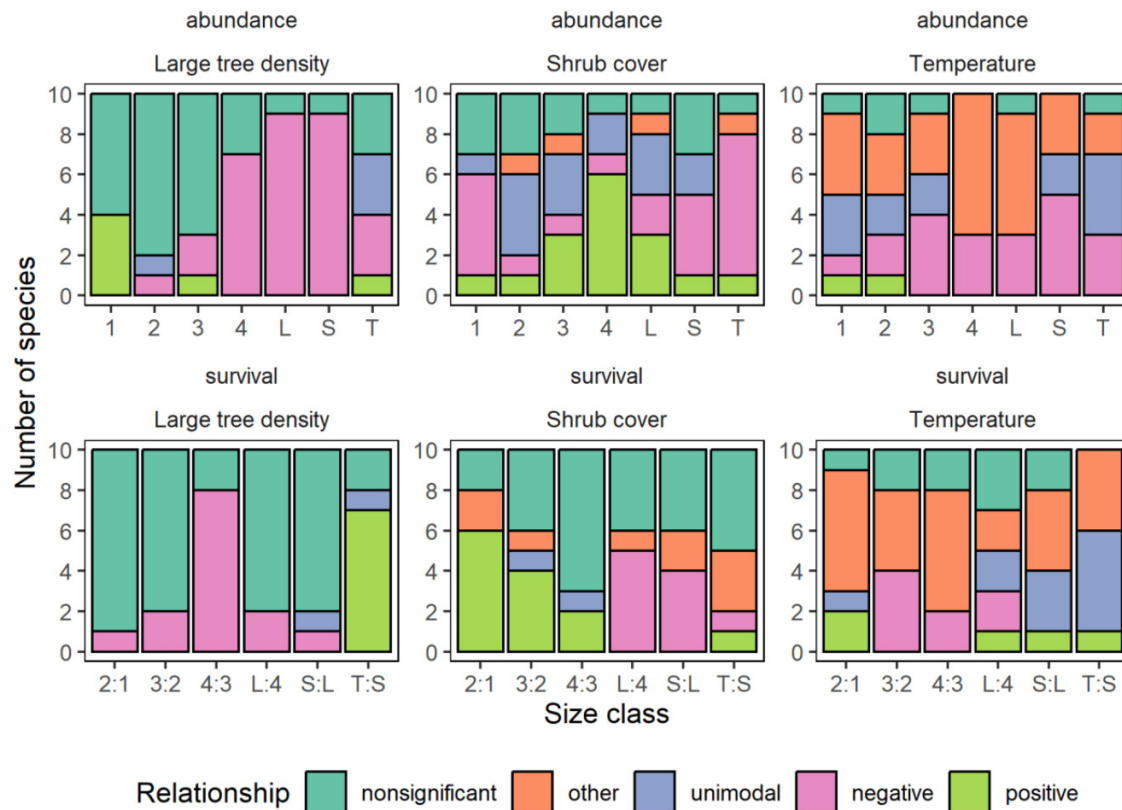


also present for each of the juvenile tree classes. This switch in shrub cover–abundance relationships from negative to positive and then back to negative was generated by positive relationships between shrub cover and seedling survival most prevalent in the Class 1 to 2 transition (six species)

offset by negative relationships from Class 4 to sapling size.

Relationships with temperature were largely significant according to our criteria (i.e., >5% of values outside the 99% CI), but almost half of these relationships did not have a

Fig. 5. Trends in the shape of relationships across species between abundance/survival and large tree density, shrub cover, and mean annual temperature. Size classes are seedling Classes 1–4. L, large seedling (Classes 5 and 6); S, sapling; T, small tree. Relationships were considered nonsignificant if >95% of values fell within the 99% confidence interval of values expected by chance.



coherent shape and were classified as “other” (Fig. 5). Although results were more varied than those for large tree density and shrub cover, unimodal relationships between temperature and abundance were most common for Class 1 seedlings (5 species), whereas 3–5 species showed negative relationships for each of Class 3 to small tree size. For survival and temperature, negative relationships were observed only from Class 2 to large seedlings, and unimodal relationships were most common at the sapling to tree transition (five species).

Trends across size classes

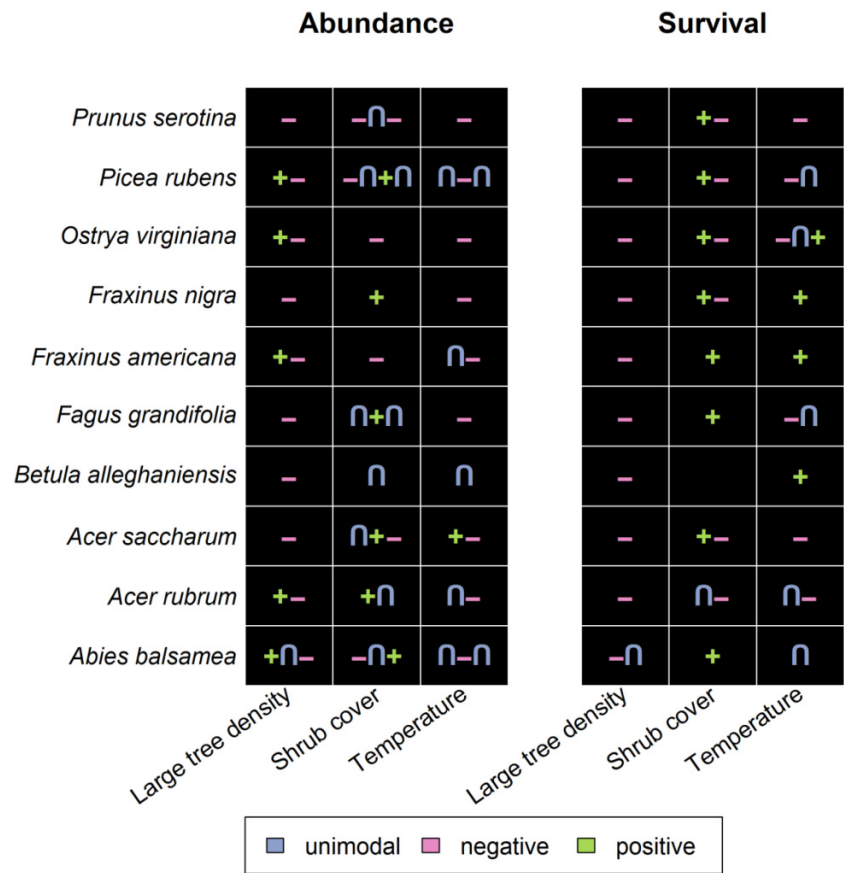
Assessing the shape of relationships within each species-variable combination revealed whether or not relationships were consistent as juvenile trees grow into successive size classes. Across all species-variable combinations, roughly half had just one type of relationship indicating consistency across juvenile tree size classes (Fig. 6). However, changes in the shape of relationships were evident in 45% of cases. Relationships between survival and large tree density were exclusively negative for 9 of 10 species, but abundance-large tree density relationships switched from positive to negative for 5 species reflecting positive relationships for small seedlings (especially Class 1) and negative relationships with larger seedlings (Class 2 and taller). Abundance-shrub cover relationships changed shape for six species, and considerable dif-

ferences among species were evident. Survival-shrub cover relationships were more similar across species; five species switched from positive relationships in the Class 1 to 2 or 2 to 3 transitions to negative relationships from Class 4 to sapling size and three species had only positive relationships. Relationships with temperature changed shape in almost half of cases, with considerable variability across species both for juvenile tree abundance and survival.

Discussion

On the path from tree seedling establishment to eventual canopy recruitment, success is determined by a set of environmental and ecological filters that may vary by life stage. Recent work highlights how key demographic processes such as fecundity, sapling and tree recruitment, and tree growth and survival differ from one another in their response to factors such as climate and competition, implying that influences on tree demography are indeed life stage-dependent (Schultz et al. 2022; Sharma et al. 2022; Yang et al. 2022). Our methodology extends this prior work by revealing how relationships with climate and vegetation vary among juvenile tree size classes, particularly within the seedling stage. The framework described here could be applied to any tree regeneration dataset for which stems are divided into size classes, yet repeated measurements

Fig. 6. Shapes of relationships (∩, unimodal; −, negative; +, positive) between abundance and survival and the three factors examined (large tree density, shrub cover, and mean annual temperature) with increasing seedling and sapling size classes. For example, “+ −” indicates a switch from a positive to negative relationship with increasing size. Relationships that were nonsignificant or not classifiable (“other”, see Fig. 5) are not shown. Note that the tree size class and tree-to-sapling ratio are excluded from this figure to focus on the tree regeneration stage.



are not available to directly assess ingrowth into these size classes.

Three key points emerged from the results. First, our methodology is useful for pinpointing the juvenile tree size classes at which demographic bottlenecks occur. For example, relationships with large tree density suggest dominantly negative effects of closed-canopy conditions on seedling survival, with the most common survival bottleneck being growth above 0.9 m tall (Class 3 to 4 transition). This finding is consistent with observations that seedlings of shade-tolerant species may persist for decades at heights of <1 m, yet recruitment to larger size classes is unlikely unless canopy gaps open (Canham 1989; Marks and Gardescu 1998). This survival bottleneck occurred at different sizes for some species; high overstory tree density did not negatively affect *Fraxinus nigra*, which has a noted ability to generate banks of tall advance regeneration (Fraver et al. 2022), until it reached 1.5 m tall. *Acer rubrum*, which is noted for seedling survival that is often lower than that of other species (Frey et al. 2007; Kobe et al. 2010), had a negative relationship between survival and large tree density for its growth up to as well as beyond 0.9 m tall. This ability to identify which size classes are demographic bottlenecks may be

useful when managing for successful recruitment at broad scales. For example, the size class and species-specific responses to overstory tree density that we observed speak to the potential utility of shelterwood methods that promote regeneration and release of particular species (Rogers et al. 2022).

A second key point is that we observed considerable within-species variability across juvenile tree size classes, including switching between positive and negative relationships in 25% of species-variable combinations. This switching was exemplified by relationships between shrub cover and survival, which switched from positive to negative for 5 of 10 species. Shrubs may facilitate survival of tree seedlings growing beneath them by protecting seedlings from temperature extremes, drought, and herbivory (Berkowitz et al. 1995; Gómez-Aparicio et al. 2004; Walters et al. 2016). These protective effects of shrubs may explain the prevalence of positive relationships that we observed for seedling survival up to 1.5 m and especially up to 0.3 m tall. However, negative relationships between shrub cover and survival prevailed for growth into the large seedling and sapling class. In the northeastern and midwestern US, where browsing is known to strongly affect tree regeneration, seedlings that

emerge above a dense shrub layer may be subjected to high-intensity browsing that could clip seedlings back to the shrub layer, reducing their competitiveness and eventually leading to seedling mortality (Whitney 1984; Puettmann and Saunders 2001). The indirect, ratio-based approach used in the present study may be an effective way to reveal how biotic interactions change with the developmental stage of trees.

The third key point emerging from the results is that patterns of abundance may mask different and sometimes opposing relationships with survival. The relationships between *Acer saccharum* and mean annual temperature illustrate this point. Looking at abundance revealed consistent negatively relationships across size classes, perhaps consistent with upslope and poleward shifts in abundance patterns due to climate change. Yet, *Acer saccharum* survival from 0.9 m tall to sapling size was positively related to temperature, and survival to tree size was unimodally related to temperature. Therefore, our results suggest that the negative relationship between temperature and *Acer saccharum* abundance arises from the seedling establishment and small seedling survival stages and that in fact the outlook for seedlings over 0.9 m tall is very different. In such cases where negative relationships between temperature and survival are limited to seedlings <0.9 m tall (also true for *Acer rubrum*, *O. virginiana*, and *Picea rubens* based on our results), management strategies targeted at early survival of seedlings, including planting seedlings that have already grown beyond the most vulnerable size classes, may help to ameliorate negative impacts of climate warming on species abundance. Additionally, the highly variable relationships that we observed with temperature across both species and size classes suggest the need for further work on how climate change may affect seedling survival and therefore future species composition. As this example shows, examining relative survival using ratios of abundance may provide useful information for predicting and managing for recruitment of key tree species.

Strengths and limitations of approach

In-depth experimental approaches are vital to determine mechanisms underpinning juvenile tree survival. Additionally, tagging and remeasuring seedlings over the course of months to years allows mortality and growth rates to be directly calculated and proximal causes of damage and mortality to be assessed (Marks and Gardescu 1998; Frey et al. 2007; Cleavitt et al. 2014). However, the cost and time commitment involved in tracking individual seedlings over time mean that these protocols cannot typically be implemented at broad scales. Novel statistical approaches that leverage existing broad-scale field data such as FIA's RI plots can assist with refining our understanding of juvenile tree development at regional scales with implications for reforestation and forest management actions at the stand scale. Compared with directly tracking the fate of individual tree seedlings over time, the ratio-based method that we demonstrate does not allow direct quantification of mortality and recruitment rates between size classes but can be applied to any sufficiently large set of field data in which seedlings are tallied by size class. As compared with more intensive tag-and-remeasure approaches, the method demonstrated here is useful for char-

acterizing associations with tree seedling abundance and survival across broad regions and sets of site conditions.

We emphasize that our approach does not investigate mechanisms behind abundance and survival. Careful interpretation of results is warranted, as suggested by the sometimes-noisy relationships that we observed with mean annual temperature. In some cases, particularly for species that tend to be found in particular topographic settings such as mountainsides or riparian settings (e.g., *Abies balsamea*, *Fraxinus nigra*, and *Picea rubens*), the gridded climate data we used may have been too coarse to accurately capture temperature influences on these species. However, mean annual temperature may also covary with climate, vegetation, soils, or other factors that influence seedling survival, meaning that some of the noise observed in the temperature relationships may be due to particular geographic areas having higher seedling abundance or survival for reasons other than temperature. Geographic variability could also arise from regional differences in management regimes that favor regeneration of certain species.

A key assumption underpinning our approach is that ratios of abundance between adjacent size classes indicate the relative rate at which individuals advance from one size class to the next. By pooling data from multiple subplots that represent a broad range of conditions when calculating these abundance ratios, we strive to avoid confounding influences such as forest successional stage. In effect, our methodology is a type of space-for-time approach (Pickett 1989) in which size class data from a large number of plots are used to make inferences about survival in lieu of longitudinal data in which individual seedlings are tracked. This key assumption seems reasonable in many cases but could be untrue in cases where the factor being examined is highly variable over time and/or itself biased by other forest characteristics that influence survival. An example of bias by forest successional stage yielding potentially misleading results is the strong positive effect that we observed of large tree density on the ratio of small trees to saplings. This result likely reflects that stands with canopy gaps and high abundance of saplings would be expected to experience self-thinning with consequently high sapling mortality rates, although the total density of new tree recruits should still be typically higher under these open conditions than under a dense overstory canopy. Indeed, our results show that maximum abundance of small trees occurred at low-moderate densities of large trees even though sapling mortality rates were higher at these densities. To some extent, examining interactions between factors may be useful for assessing potentially confounding influences. Although our purpose in this analysis was simply to demonstrate this ratio-based approach rather than systematically evaluating the factors that can be examined with it, interrogating its underlying assumptions in more depth would be a good topic for future work.

Conclusions

In the context of changing climate, disturbance regimes, invasive species, and other global change drivers, successful tree regeneration of key species in forests is a concern even

in regions such as the northeastern US where tree regeneration has not traditionally been closely monitored or managed (Dey et al. 2019). By looking across species, we found common trends in relationships with abundance and survival and identified which size class transitions appear to be most critical for juvenile tree survival (e.g., Class 3 to 4 for large tree density and Class 1 to 2 for shrub cover). By looking across size classes, we identified a substantial number of species-variable combinations for which relationships changed over juvenile tree size classes. These switches imply that key influences on juvenile tree abundance and survival may vary substantially by size, which has implications for monitoring and managing tree regeneration in the context of global change. Our results suggest that influences of climate and vegetation on abundance and survival can change dramatically across juvenile tree size classes for a given species and underscores the need for further work on how environmental filters determining survival and growth vary as trees develop.

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Data availability

The forest inventory data that support this study are publicly available from the USDA Forest Service FIA DataMart (<https://apps.fs.usda.gov/fia/datamart/datamart.html>). Code is available upon request.

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Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjfr-2023-0097>.

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