Abstract. Changing climatic regimes are causing increasing temperatures, changing precipitation patterns, and are subsequently expected to impact the spatial distribution of species. The distribution of plants at the scale of continents broadly conforms to the climatological regimes at play; however, in scaling down to the regional and landscape context, the influence of climate becomes confounded by complex and interacting biotic and abiotic factors. These factors have often been cited as important variables in determining the locations of biome overlap, including the boreal forest–temperate forest ecotone (BTE). The BTE exists as a broad latitudinal swath between the boreal and temperate forest biomes in the eastern half of North America. While the impact of non-climatic factors on the location of the BTE has been investigated within the ecotone, few studies focus on how these same factors are shaping the colonization of the southern boreal forest by northern temperate tree species as part of a potential northward shift of the BTE. The effects of seed and seedling herbivory, substrate composition, microclimate, and canopy composition on seedling emergence of four northern temperate tree species were investigated in a beyond-range seeding experiment spanning the southern portion of the island of Newfoundland, Canada. To represent a range of temperate tree reproductive strategies, we examined two small-seeded tree species, Betula alleghaniensis and Thuja occidentalis, and two tree species with large seeds relative to typical boreal forest species, Acer saccharum and Fraxinus nigra. The results of this experiment show a reproductive strategy-dependent emergence response; large seeds and seedlings appear more vulnerable to predation, while small seeds are more vulnerable to smothering by leaf litter. Canopies with greater representation of deciduous species posed a significant barrier to small seeds that produce small seedlings, while the food-rich reward of the larger seeds made for attractive targets to granivorous vertebrates. This work represents a rare glimpse at the challenges northern temperate tree species will face if they are to colonize the southern boreal forest and track changing climates as is broadly expected.

Key words: boreal temperate ecotone; canopy composition; ecological filter; ecotone; emergence; exclosure; forest; germination bottleneck; range expansion; seed herbivory; substrate.

INTRODUCTION

Species’ range shifts are expected in response to changing climate regimes, but only insofar as their inherent biotic and abiotic limitations will allow (Lafleur et al. 2010, Parmesan and Hanley 2015). For many species, the implications of climate change will mean uncolonized habitat patches beyond their current range edges may become environmentally suitable (Iverson and Prasad 2002, McKenney et al. 2007). Yet, a climatological approach alone is not enough to understand how range expansion will proceed and does not elucidate the complexities with which...
species’ range shifts are, and will be, occurring (HilleRisLambers et al. 2013, Evans and Brown 2017). In particular, biotic interactions are important modifiers of climate-induced distributional shifts (Brooker et al. 2007, Zarnetske et al. 2012, Urban et al. 2013) and can create legacy effects in the potentially invaded ecosystem, where the established community presents few remaining available niche spaces for invader’s to occupy (Westman 1978, Pielou 1991). Bigelow and Canham (2015) provide evidence for this in ecolonial forest stands, in which interactions between stand composition, litterfall, and soil create niche space that appears to favor conspecific seedling establishment.

Despite our understanding of the importance of biotic interactions in determining where species may establish, disentangling climatic and non-climatic effects along the gradients over which range edges typically occur is difficult. Independently, abiotic factors of soil and climate are each multi-faceted drivers of species ranges; however, these must also be understood with the third dimension of soil microbiota and soil–climate–biotic interactions (Lafluer et al. 2010). The inclusion of few (soil type and drainage, e.g., Chambers et al. 2013) or many (texture, drainage, chemical, cation exchange capability, and pH, e.g., Figueiredo et al. 2018) factors in species distribution model studies seeking current and future tree species ranges tends to improve model accuracy in the face of uncertainties posed by climate change projections. Soil is just one example of many complex interactions; the list includes interacting climate–pest species (Logan et al. 2003), climate–disturbance regimes (Rocca et al. 2014), and plant–pollinator phenological mismatching (Hegland et al. 2009), to name a few.

Trees are long-lived, habitat-forming organisms (Thomsen et al. 2010), and their presence, absence, and abundance are reflective of century-to millennium-scale climate regimes. Repeated southward and northward range shifts have been documented in concert with dramatic, large-scale climatic swings during glacial events (Comes and Kadereit 1998, Svenning and Skov 2007) and shorter, more localized climatic events, such as the Little Ice Age (Hupy and Yansa 2009). Contemporary, localized range shifts have been documented globally (Davis and Shaw 2001).

Ongoing shifts are occurring with some populations of temperate tree species invading the trailing edge of the boreal forest at the boreal–temperate forest ecotone of North America (Evans and Brown 2017) and populations of northern edge boreal forest trees invading the tundra and alpine regions at the forest–tundra ecotone (Harsch et al. 2009). Yet, climate-induced range shifts of tree species are not ubiquitous across their distributional limits (Harsch et al. 2009, Evans and Brown 2017). Species’ life history strategies are selected for, and adapted to, the pressures exerted upon them by the system in which they persist. As species, such as trees, attempt to colonize new systems in response to climate change, the strategies that succeeded in their historic distribution may not be well suited to the new conditions, contributing to the ecological inertia of the existing ecosystem. Additional challenges are presented in dispersal-limited settings, where the unlikelihood of genotypes with good chances of survival under specific novel conditions arriving and establishing a local population (i.e., right genotype in the right place at the right time) is compounded (Kawecki and Ebert 2004). Further constrictions on the path toward establishing a new population in these settings are imposed if the source gene pool is small and/or has already undergone selection for conditions at native distribution extremes. For example, producing large seeds in a boreal forest community in which small seeds are the norm may be detrimental to seed survival due to predation selection (Zhang et al., 2005).

The boreal–temperate ecotone (BTE) is the transition zone wherein the northern extent of the temperate forest overlaps with the southern extent of the boreal forest; it occurs in eastern North America, northeastern Europe, and eastern Asia (Goldblum and Rigg 2010, Evans and Brown 2017). This transition generally occurs along a north–south gradient where both tree species diversity and average annual temperature decrease with increasing latitudes, with thermal conditions often considered the primary factor determining the ecotone’s location (Arris and Eagleson 1989). A more comprehensive suite of factors are explored by Ahti et al. (1968), Pastor and Mladenoff (1992), Svenning and Skov (2005), Goldblum and Rigg (2010), Pastor (2016), and others. In North America, the BTE is at its
widest and occupies a zonal band from southeastern Manitoba to the Gaspé Peninsula, Quebec, and from western Minnesota to Cape Breton Island, Nova Scotia (Olson et al. 2001, Goldblum and Rigg 2010). Despite portions of Newfoundland, a large island in eastern Canada, falling within the BTE latitudinal zone and possessing similar climatic characteristics to mainland areas of the BTE (Agriculture and Agri-Food Canada and Government of Canada 2019), the expected species assemblages are not found there. The most parsimonious explanation for this pattern is the approximately 110 km wide Cabot Strait that isolates southwestern Newfoundland from Cape Breton Island, the eastern-most distributional range of many temperate tree species (Farrar 1995). However, as this dispersal barrier becomes functionally smaller due to anthropogenic transport of propagules, the probability of successful species colonization events is increasing.

Research approach

Colonizing tree species face a variety of barriers that act to filter out individuals from an establishing population, but few studies have tied together biotic and abiotic variables within the same study to test these filters in novel habitats (Urban et al. 2012, Hargreaves et al. 2014, Putnam and Reich 2017, Solarik et al. 2018). Here, we address the earliest and most vulnerable life-stages of tree species in a beyond-range setting on Newfoundland, Canada, allowing us to assess how biotic and abiotic factors influence species’ range limits. We explicitly addressed four hypotheses of temperate tree seedling emergence success at, or beyond the range edge using field experimentation. We hypothesized that seedling emergence success would be maximized if seeds and resultant seedlings were (1) protected from vertebrate herbivory pressure, (2) under mixed coniferous-deciduous canopy compositions resembling those found within the distributional range, and (3) on a leaf-litter dominated substrate corresponding with the aforementioned mixed canopy composition.

To test these hypotheses, we used four model temperate tree species whose early life history strategies vary drastically: (i) two species that produce large seeds relative to boreal species, one native to Newfoundland, black ash (Fraxinus nigra Marsh.), and one native to mainland Canada, but only found in Newfoundland as an ornamental, sugar maple (Acer saccharum Marsh.); and (ii) two small-seeded species, again a native species, yellow birch (Betula alleghaniensis Britt.), and another common ornamental, eastern white cedar (Thuja occidentalis L.). These model species are representative of the BTE, each with significant portions of their native distributions falling within the geographic area of this ecotone (Goldblum and Rigg 2010, Evans and Brown 2017). The two model species with no natural distribution on the island (Farrar 1995) enabled us to test a fourth hypothesis, which takes similar form to that of McCarragher et al. (2011): (4) Emergence success beyond the range edge will be positively associated with seed provenances from harsher plant hardiness zones, as adaptations to climatic conditions are often inherited (Aitken et al. 2008, Solarik et al. 2016).

We expected to see greater successful seedling emergence of large-seeded model species that were protected from seed herbivory by small vertebrates (Brown and Vellend 2014), while we expected response to the substrate type and canopy composition would be modest. Alternatively, we expected that successful emergence for small-seeded model species would be positively associated with mossy substrate and predominantly coniferous canopy cover, due to the risk of seedling smothering under the leaf litter in a mixed forest (Buda et al. 2011). We also investigated whether climate was linked to successful emergence patterns of our model species; we hypothesized that an earlier frost-free date and warm early season temperatures would result in greatest emergence success for all model species (Appendix S2: Table S1; Vanstone 1974, Perala and Alm 1990, Bonner and Karrfalt 2008, Larouche et al. 2011, Solarik et al. 2016).

The goal of our work was to build an understanding of how northern temperate tree species’ establishment in boreal forest stands is affected by interacting abiotic and biotic factors. We were interested in how the ecological inertia of boreal forest stands mitigates the distributional advance of temperate tree species under ongoing climate change. Our research was unique in that it took place in a relatively isolated island boreal forest system that will share increasingly similar climatic conditions to temperate tree species’ historic, mainland distributions. Here, we present
our findings from a series of ecological field experiments in which we simulate the beginning stages of colonization of boreal forest stands by temperate tree species, with the aim of disentangling the biotic and abiotic factors contributing to their colonization success, or lack thereof.

**Methods**

*Study area*

Newfoundland is projected to see widespread increases in mean temperature and annual precipitation by mid-late century (Finnis 2013, Natural Resources Canada 2015). Mean annual precipitation and temperature are expected to rise across Atlantic Canada, with Newfoundland tracking or exceeding the Maritime provinces’ rate of precipitation and temperature increases, respectively (Natural Resources Canada 2015). Southern Newfoundland could see a mean annual temperature increase of 1.5–3.1°C, an increase in annual growing degree days (GDD) of 108–211 ($T_{\text{base}} = 10^\circ C$), and an annual frost-free period increase by 27–35 d by 2070 (Finnis 2013). Newfoundland’s geographic position combined with its climate change projections makes it an ideal location for studying climate change effects on forest composition, especially given the already abundant diversity of tree species introduced to the island through anthropogenic means, particularly in the island’s urban centers (Environmental Design and Management 2006). Modern tree species range shifts have not been studied in Newfoundland in the context of a changing climate (Evans and Brown 2017), and the island’s physical separation from mainland North America creates an interesting natural experiment to examine confounding variables affecting possible species’ range shifts.

Our study was initiated in 2015 (phase 1, seedling emergence in f except $F. nigra$ in 2017); in 2016, we duplicated and expanded the experiment (phase 2, seedling emergence in 2017) while maintaining the same core experimental design for all species, except $F. nigra$ that takes two years to germinate under natural conditions. Variations in our methodological approach between the two phases of the experiment meant that data were analyzed separately.

Southern Newfoundland experiences a humid, snowy climate with warm summers (Köppen climate classification: Dfb; Kottek et al. 2006) and contains 8 of the island’s 9 ecoregions (Damman 1983). Sites were selected based on a number of criteria (Appendix S2: Table S2): (1) on public (Crown) land that would not be logged for a minimum of three years, or on Provincial (i.e., Provincial Parks), or private lands with permission from the landowner, (2) were within 1 km of a publicly accessible road, and (3) contained stands of mature boreal coniferous forest (boreal forest type; forest type selection described below) and mixed coniferous–deciduous forest (mixed forest type) with no evidence of recent harvesting in close proximity. Sites with non-native tree species present were avoided.

*Model species*

These four tree species are well suited to the climatic conditions found on much of the southern portion of Newfoundland, having already colonized areas with similar climates in mainland Canada (Farrar 1995) but may be vulnerable to the variable spring weather and typically late frosts common to the island (Environment and Climate Change Canada 2017).

*A. saccharum* produces large seeds relative to typical boreal species (see Appendix S1 for full species descriptions), which allow for vigorous germination (Yawney and Clayton 1968) but also make the seeds vulnerable to predation in boreal forest communities (Brown and Vellend 2014). $F. nigra$ produces seeds with large samara but has immature embryos that require specific climatic conditions over periods of up to two years to mature and break dormancy (Vanstone 1974), allowing abundant time for dispersal, predation, and/or seed desiccation. *B. alleghaniensis* and *T. occidentalis* share several early life history traits; they are both small-seeded species, facilitating wind dispersal. Both the latter species germinate rapidly in suitable conditions, but their small seed size means they must quickly acquire moisture and nutrients from the seedbed after germination (Cornett et al. 2000, Caspersen and Saprunoff 2005) and are vulnerable to smothering under leaf litter (Burton et al. 1969, Buda et al. 2011).

*Experimental design*

Our core experimental design, constant across phases 1 and 2, manipulated (1) herbivore access...
duplicated, and a further three sites (Appendix S2: Table S2). These sites during the second phase of the experiment involved experimental treatment setup and seedling emergence, took place between 12 and 19 September 2015 (phase 1) and 15 and 22 October 2016 (phase 2). Each pot was inspected closely for the presence of seedlings, seedling and seed (if found) health, and general pot condition. Seedlings were counted as having emerged if the radicle had breached the seed coat. Seed and seedling herbivory were recorded qualitatively based on the presence or absence of evidence of herbivory. Some pots were lost due to moose trampling or were obliterated by snow crushing, which disproportionately affected uncaged pots (n = 38) over caged pots (n = 15; see Evans et al. 2018 for cage effects). Several A. saccharum and T. occidentalis (n = 12 each), and B. alleghaniensis (n = 7) pots seeded in phase 1 were unable to be relocated in May 2016. All phase 2 pots were accounted for in summer 2017 (n = 480 each).

Substrate composition.—To isolate the effects of forest type and substrate composition on emergence success, forest floor substrate was reciprocally transplanted between forest types within each site. Using a soil knife, the first 10–15 cm of soil and substrate was removed from the forest floor and inserted into peat pots (14.5 × 12.5 cm), efforts were made to maintain the soil–substrate structure during removal and transport. Pots of substrate were then either reinserted into the ground in place or transported to and planted in the other stand type; this way the local and imported substrate type were tested under both canopy types. To test for any influence of the pot itself on seedling emergence, we installed a control treatment where pot rims (top 1/3 of peat pot) were inserted into the soil to contain the planted seeds, but the substrate was otherwise left undisturbed.

Herbivory exclusion.—In both phases 1 and 2, half of the pots deployed were placed within cages that were designed to limit seeds’ exposure to small terrestrial vertebrate herbivores. Phase 1 exclosure cages, measuring 50 (h) × 122 (l) × 81 cm (w) and encased in 6.4 × 6.4 mm hardware cloth (see Evans et al. 2018: Fig. 2b), had a closed-top design similar to other
exclosure cage designs that have been used (Côté et al. 2003, Munier et al. 2010). Observations and qualitative data revealed challenges with our phase 1 herbivory exclusion methods, where the closed-top design tended to block the passage of leaf litter and snow entering the cage (described in detail in Evans et al. 2018). While not all sites were accessible during the winter months, it is assumed that all phase 1 cages had this issue. In response, we switched to an open-top exclosure cage design in phase 2, which is similar to designs where the differential impact of rodent versus bird granivores was evaluated (Howe et al. 2002). Phase 2 exclosure cages were 92 (h) × 56 cm diameter (Ø) cylinders of 2.5-cm galvanized chicken wire with a 31 (h) × 56 cm Ø cylinder of 6.4 × 6.4 mm hardware cloth wrapped around the bottom third of the chicken wire in order to deter small vertebrates (see Evans et al. 2018: Fig. 2c). A strip of flexible plastic was attached to the top portion of the cage in an effort to deter climbing vertebrates. The change in design required that data were analyzed separately for the two phases of the experiment, as described below. Neither cage type was designed to withstand interactions with large herbivores, such as moose, or to prevent access to invertebrates.

**Seeding.**—Pots were seeded immediately following site establishment between 12 and 19 September 2015 (phase 1) and 15 and 22 October 2016 (phase 2), within the natural seed-fall period of all model species (Burns and Honkala 1990). In all cases, seeds were dropped evenly across the substrate within the pot. In phase 1, each block contained the following array of pots per treatment combination: two pots sown with *A. saccharum* (each pot contained a different
provenance, explained further below; \( n = 5 \) seeds/pot), two sown with *T. occidentalis* (two provenances; \( n = 10 \) seeds/pot), one sown with *F. nigra* (\( n = 5 \) seeds/pot), and one sown with *B. alleghaniensis* seeds (\( n = 10 \) seeds/pot), for a total of 36 seeded pots per block (six pots \( \times \) six treatment combinations). These numbers were standardized for the phase 2 seed sowing; 10 seeds of each species were sown into one pot per treatment combination, reducing the number of pots to 24 per block (four pots \( \times \) six treatment combinations). Note that the germination requirements of *F. nigra* meant that the seed sown in 2015 did not germinate until 2017 but were still considered part of phase 1. All seed was obtained from the National Tree Seed Centre (NTSC; Fredericton, NB, Canada) from seed sources in New Brunswick and Nova Scotia. Attempts were made to use highly viable seed stock from regions with climates as similar to Newfoundland as possible to maximize local adaptation to the potentially difficult climatic conditions model species would encounter in Newfoundland (Appendix S2: Table S3). In several cases, our requirement for seed to be of geographically similar provenance (i.e., from Atlantic Canada) limited availability of recently collected seed (Appendix S2: Table S3). While

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Fig. 2. Experimental design diagram showing (a) conceptualized difference in canopy composition between boreal and ecotone forest types (left and right, respectively) and (b) planting block layout shown within one of the two forest types within each site. Blocks are approximately \( 2 \times 2 \) m in dimension, spaced at least 1 m apart (c). The blocks shown in (c) show the round open-top cages deployed in phase 2 and contain 24 pots per block, rather than the closed-top box cages deployed at each block in phase 1, which had 36 pots. Each species was planted in a caged or control pot containing boreal or ecotone soil, or in a control pot, which were the top one-third of a pot seated into the local soil (d). Abbreviations are F, *F. nigra*; B, *B. alleghaniensis*; A, *A. saccharum*; and T, *T. occidentalis*. 

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many temperate species’ seeds have good longevity when stored under the correct conditions (Bonner 1990), obtaining recently collected seed for our model species from Atlantic Canada was a challenge. Seeds from multiple seed lots were requested in order to achieve higher overall germination rates in order to mollify this challenge (Appendix S2: Table S3).

The phase 1 experimental design included an additional treatment for A. saccharum and T. occidentalis to investigate whether seed source would imbue beneficial climatic adaptations for the climate beyond the species’ natural distribution. Seeds for these model species were sourced from areas in either warm plant hardiness zones (>4) or cold hardiness zones (<4; Agriculture and Agri-Food Canada 2000) in order to see whether variations in adaptation in the parent individuals would be beneficial for seed germination under a more challenging climate, as others have investigated (e.g., McCarragher et al. 2011, Solarik et al. 2016). Models, which included seed provenance as an explanatory variable, fit to phase 1 A. saccharum and T. occidentalis emergence data showed support that provenance had an effect on A. saccharum but not T. occidentalis seedling emergence (Appendix S2: Table S7). Contrary to our predictions, warm provenance A. saccharum seeds had increased emergence success over cold provenance seeds. Nevertheless, our focus in phase 2 shifted to investigate the role of reproductive strategy in our model species’ success, rather than provenance. Ultimately, all phase 1 A. saccharum and T. occidentalis seeds were considered the same for treatment variable analyses (i.e., provenance was ignored) and hypotheses tested (using both phases 1 and 2 emergence data) centered around relative seed size, whereby A. saccharum and F. nigra have relatively large seeds, while B. alleghaniensis and T. occidentalis have similar-sized seeds when compared to boreal forest species on the island.

Climate.—To provide continuous environmental monitoring, two climate sensor arrays were installed at each site, one within each forest type, in October 2016. The climate sensor arrays were composed of Onset HOBO Data Loggers Micro Station Logger with Smart Temperature Sensor, Soil Moisture Smart Sensor, and Temperature & RH Sensor (Onset Computer, Cape Cod, Massachusetts, USA) assembled onto approximately 1 m tall masts. Air and soil temperature, relative humidity, and soil moisture readings were sampled at 1-h intervals from the time of seeding (October 2016) through the end of the 2017 growing season (final data collection: September 2017).

Statistical analyses

Seedling emergence data were partitioned into presence/absence (presence data) and proportion of successful emergent seedlings (abundance data; Fig. 3; after Tsuyuzaki et al. 2014). Partitioning the response variable this way allowed us to identify variables (see Appendix S2: Tables S1 and S4 for predicted responses and explanatory variable details, respectively), or combinations thereof, driving (1) whether the seedlings emerged at all, and (2) conditions that promoted the greatest number of emergent seedlings in a given pot, respectively (Zuur et al. 2009). Emergence datasets from 2016 and 2017 for each species were used for response variable × treatment analysis (Appendix S2: Table S1). We analyzed presence and abundance data for the 2016 and 2017 emergence years separately, fitting generalized linear mixed-effects models with a binomial error structure and logit link for the presence, and zero-inflated binomial models for abundance response variables with treatment explanatory variables (herein, treatment analysis).

During seedling emergence surveys in 2017, we observed and counted naturally occurring first-year Betula sp. (B. alleghaniensis and B. papyrifera) seedlings in pots not seeded with B. alleghaniensis (n = 1,440). This allowed us to account for background contamination of natural Betula sp. seedling emergence when performing analysis on phase 2 data (Fig. 3). This correction was only applied to the 2017 emergence data due to the infrequency of site visits in 2016, which did not allow for accurate tracking of naturally occurring Betula sp. emergence.

Statistical analyses were performed using model selection based on corrected Akaike Information Criterion (AICc; Hurvich and Tsai 1989, Akaike 1998, Burnham and Anderson 2004) for small sample sizes. Following Burnham and Anderson (2003, 2004), we considered models with ΔAICc ≤ 2 to have essentially as much explanatory power as the top-ranked model (i.e.,
ΔAICc = 0), models with a ΔAICc between 4 and 7 are considerably weaker, and models with ΔAICc > 7 have very little support. We employed the small-sample AICc method of model selection, as many of the global models fitted to our species-specific datasets were at or near the n/K > 40 approximate threshold, at which AICc begins to converge to AIC (Burnham and Anderson 2004).

All possible combinations of treatment variables were fitted to data for each species for each emergence year. This approach allowed us to test our hypothesis that biotic and abiotic drivers of emergence within a species’ range are important beyond their range (Table 1; Murtaugh 2007, Symonds and Moussalli 2011). To account for the hierarchical structure of our experimental design, the models created for all hypothesis testing included block nested within site as a random effect, and each model set included a model with only this nested random term (i.e., hereafter the Null model; Bolker et al. 2009) for a total of eight candidate models per species. For models in which substrate type was included as an explanatory variable, an additional random effect was included, designating each pot as either treatment or control to account for variability introduced by the substrate treatment method itself. Data for canopy composition were standardized to account for the difference in scales between categorical and continuous variables by subtracting the variable mean from each value and dividing that result by its standard deviation (Appendix S2: Table S4). Although there is the risk of finding importance in variables with little support in small datasets, as outlined in Freedman’s Paradox (Freedman 1983), the model variables we used represent important ecological relationships for these species within their range limits; therefore, we assume that they will still be important in the novel environments represented in our study.

Analyses were carried out using the R Project statistical software (version 3.3.2; R Core Team 2016) packages nlme (Pinheiro et al. 2017), mctest (Ullah and Aslam 2017), glmmer (Magnusson et al. 2017, Brooks et al. 2017), and bbmle (Bolker and R Core Team 2016). Pseudo-R² values for binomial models were calculated after McFadden (1973). A confidence set of best-supported models was created for each combination of species × response variable for each emergence year and was populated by fitted models with a ΔAICc < 2. We removed models containing difficult-to-interpret parameters (Burnham and Anderson 2004).
Table 1. Full candidate model set applied to presence and abundance data for each model species’ emergence data for each year in which germination occurred.

| Model | Predictor variables |
|-------|---------------------|
| 1     | 1 + (1 | Site/Block) |
| 2     | %DecC + (1 | Site/Block) |
| 3     | XPred + (1 | Site/Block) |
| 4     | SubM + (1 | Site/Block) |
| 5     | XPred + %DecC + (1 | Site/Block) |
| 6     | XPred + SubM + (1 | Site/Block) |
| 7     | SubM + %DecC + (1 | Site/Block) |
| 8     | %DecC + SubM + XPred + (1 | Site/Block) |

Notes: Predictor variables refer to the percent deciduous canopy cover (%DecC), protection from or exposure to vertebrate herbivory (XPred), and whether the seeds were sown onto mixed or boreal forest substrate (SubM). All models were given the nested random terms grouping Blocks within their respective Sites, to account for correlations due to geographic proximity.

Results

Seedlings emerged consistently across the two phases of the experiment, but with considerable variation in the success of species across sites and between emergence years (Tables 2, 3). F. nigra emergence was greatest of the model species and was most abundant in sites within its natural distribution on the island (Farrar 1995), that is, western sites (e.g., 15A; Table 2; recall: sown in 2015, emerged in 2017). In contrast, T. occidentalis had the lowest emergence of the model species, albeit the proportion of emerged seedling increased between the two phases of the experiment. A. saccharum emergence was variable across sites (0.5–63.5% site-level emergence; Table 2) and years, with an overall increase in emergent seedling abundance in the second phase of the experiment (Table 3). Finally, B. alleghaniensis declined between the two phases of the experiment, likely due to the application of the correction factor for background contamination, which could not be applied to the 2016 data.

Seedling emergence of all model species in both emergence years was greatest when terrestrial vertebrate herbivores were excluded. Additional treatment effects varied by species and emergence year. Canopy (i.e., stand) composition had differential effects on the model species, where small-seeded B. alleghaniensis and T. occidentalis were predominately negatively associated with mixed forest stands. Evidence of a substrate treatment effect was generally weak, with the exception of B. alleghaniensis presence and abundance in 2016. Key highlights of treatment and microclimate effects follow, below.

Herbivore exclusion

Seeds.—Missing seeds were observed in 80% of uncaged pots A. saccharum in May 2016 and 55% of uncaged A. saccharum pots in May 2017. In contrast, during the June 2017 site visit, missing seeds were observed in only 3% of uncaged F. nigra pots seeded during phase 1, but that increased to 53% in pots seeded with F. nigra as part of phase 2. B. alleghaniensis and
T. occidentalis seeds were too small to accurately relocate under our field conditions; thus, those data are not included here.

Emergent seedlings.—Emergence was positively associated with the exclusion of terrestrial vertebrate herbivores for most combinations of species x response variable in either emergence year (Tables 4, 5; Fig. 4a–g). Models containing this variable also tended to have the most explanatory power, particularly for A. saccharum (pseudo-$R^2$ up to 0.15; Fig. 4a,d). Herbivory arose as the most important explanatory variable for B. alleghaniensis and T. occidentalis seedling presence in 2016 (Fig. 4b,c; pseudo-$R^2=0.05$ for both), and for explaining the abundance of seedlings when paired with substrate effects for B. alleghaniensis (pseudo-$R^2 = 0.07$), or on its own for T. occidentalis (pseudo-$R^2 = 0.04$). However, exclusion of small terrestrial vertebrate herbivores became less important for both small-seeded species’ emergence in 2017, being more often negatively correlated with emergence (T. occidentalis; Fig. 4f), or of questionable importance given the parameter estimate’s standard error (B. alleghaniensis; Fig. 4e; Appendix S2: Table S6). Support for the importance of herbivory for F. nigra was less clear; while vertebrate herbivore exclusion was an important variable in our models, it had low explanatory power (Fig. 4g, Table 4).

The change in cage design between experiment phases from closed-top box cage (see Evans et al. 2018: Fig. 2b) in phase 1 to the open-top round cage (see Evans et al. 2018: Fig. 2c) in phase 2 also came with an apparent shift in cage efficacy. Beyond the effects explored by Evans et al. (2018), the difference in the proportion of total emergent seedlings (all species) between within-cage pots and in control pots decreased from 55.4% in phase 1 to 8.2% in phase 2, with caged pots containing 77.7% and 54.1% of emergent seedlings in phases 1 and 2, respectively.

Other herbivores.—While invertebrate herbivory was not a planned focus of our study and cages were not designed to exclude invertebrates, suspected invertebrate damage was observed in up

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**Table 2.** Proportion (%) of seeds of each model species that emerged at each site in each germination year.

| Species        | 2016 |          |          |          |          | 2017 |          |          |          |          |          |
|----------------|------|----------|----------|----------|----------|------|----------|----------|----------|----------|----------|
|                | 15A  | 15B      | 15C      | 15D      | 15E      |      | 15A      | 15B      | 15C      | 15D      | 15E      |
| A. saccharum   | 7.5  | 12.3     | 11.3     | 11.8     | 1.0      |      | 1.8      | 0.5      | 0.2      | 63.5     | 0.8      | 39.0     | 2.0      | 3.2      |
| B. alleghaniensis | 5.3  | 8.6      | 1.2      | 4.8      | 4.7      |      | 0.1      | 2.5      | 2.5      | 11.3     | 7.6      | 3.3      | 2.8      | 0.1      |
| F. nigra       | ...  | ...      | ...      | ...      | ...      |      | 41.0     | 34.0     | 23.0     | 25.7     | 8.0      | ...      | ...      | ...      |
| T. occidentalis| 0.8  | 1.1      | 0.3      | 0.8      | 0.8      |      | 2.8      | 1.8      | 1.5      | 3.8      | 1.3      | 1.2      | 3.2      | 0.7      |

Notes: The number of seeds sown at each site per species varied in phase 1 (600 each for A. saccharum and B. alleghaniensis, 300 for F. nigra, and 1200 for T. occidentalis), but remained constant at 600 seeds/species/site in phase 2. Seeds sown in phase 1 are represented in the 2016 emergence year with the exception of F. nigra, which emerged in 2017 due to the lengthy seed maturation process. Ellipses indicate that no germination occurred due to the period over which this process takes place. Proportions given for B. alleghaniensis are corrected for background contamination from naturally occurring birch seed in 2017 only.

**Table 3.** Proportion of total (%) and total number (N) of pots in which seedlings were found (Presence) and emergent seedlings observed (Abundance) in both emergence years for each species.

| Species        | 2016 |          |          |          |          | 2017 |          |          |          |          |          |
|----------------|------|----------|----------|----------|----------|------|----------|----------|----------|----------|----------|
|                | %    | N        | %        | N        |          |      | %        | N        | %        | N        |
| A. saccharum   | 29.0 | 600      | 8.8      | 3000     |          |      | 25.0     | 480      | 13.9     | 4,800    |
| B. alleghaniensis | 28.0 | 300      | 5.4      | 3000     |          |      | 10.4     | 480      | 2.0      | 4,800    |
| F. nigra       | ...  | ...      | ...      | ...      |          |      | 61.0     | 300      | 26.3     | 1,500    |
| T. occidentalis| 15.0 | 600      | 0.7      | 6000     |          |      | 15.8     | 480      | 2.0      | 4,800    |

Notes: Numbers shown for B. alleghaniensis are corrected for background contamination from naturally occurring birch seed in 2017 only. Ellipses indicate no germination due to the period over which the F. nigra seed maturation process takes place.
to 41% of caged and 32% of uncaged *A. saccharum* pots in 2017, and was particularly evident for *A. saccharum*. Invertebrate damage was recorded if only part of the seedling was damaged (e.g., hypocotyl bitten in half, part or whole cotyledons or leaves eaten; sensu Meiners and Handel 2000), or if only part of the seed was damaged (e.g., holes in seed coat, cracked seed coat with all or part of the radicle or cotyledons eaten; sensu Nystrand and Granström 2000).

**Canopy type**

More *B. alleghaniensis* and *T. occidentalis* seedlings emerged in boreal forest stands (*n* = 106...
and 35, respectively) than mixed forest stands (n = 42 and 8, respectively) in both emergence years. The 2017 presence and abundance of B. alleghaniensis and T. occidentalis were both negatively correlated with increasingly deciduous canopy composition (Fig. 5c,d; Tables 4 and 5), but in neither case was there enough evidence to greatly improve the log likelihood of the

### Table 5. Model results for treatment variable analysis of abundance data.

| Model | Model weight | Predictor | %DecC | k | LogL | ΔAICc | AICcw | ER | ER0 | R² |
|-------|--------------|-----------|-------|---|------|-------|-------|----|-----|----|
| **A. saccharum (ZIB; N = 588, 480)** | | | | | | | | | | |
| 2016  | | | | | | | | | | |
| 3     | 5            | ↑         | 5     | 5 | -452.8 | 0     | 0.42  | 1.2 | 9.4 × 10¹⁹ | 0.06 |
| 5     | ↑            | ↑         | 6     | 6 | -452.0 | 0.4   | 0.34  | 3.4 | 7.7 × 10¹⁹ | 0.10 |
| 6     | ↑            | ↑         | 7     | 7 | -451.8 | 2.1   | 0.14  | 0.14 |
| 8     | ↑            | ↑         | 8     | 8 | -451.2 | 2.9   | 0.10  | 0.10 |
| Null  |              |           | 4     | 4 | -499.8 | 92.1  | <0.001|     |     |
| 2017  | | | | | | | | | | |
| 5     | 10           | ↑         | ↓     | 6 | -417.5 | 0     | 0.64  | 3.0 | 1.1 × 10⁴  | 0.02 |
| 2     |              | ↓         | 5     | 5 | -419.7 | 2.2   | 0.21  | 0.21 |
| Null  |              |           | 4     | 4 | -426.6 | 14.0  | <0.001|     |     |
| **B. alleghaniensis (ZIB; N = 293, 480)** | | | | | | | | | | |
| 2016  | | | | | | | | | | |
| 6     | 10           | ↑         | ↑     | 7 | -240.6 | 0     | 0.71  | 2.5 | 2.4 × 10⁶  | 0.07 |
| Null  |              |           | 4     | 4 | -258.5 | 29.5  | <0.001|     |     |
| 2017  | | | | | | | | | | |
| 5     | 10           | ↑         | ↓     | 6 | -353.6 | 0     | 0.49  | 1.7 | 647.6       | 0.02 |
| 2     |              | ↓         | 5     | 5 | -355.2 | 1.1   | 0.29  | 0.29 |
| Null  |              |           | 4     | 4 | -362.2 | 13.0  | <0.001|     |     |
| **T. occidentalis (ZIB; N = 588, 480)** | | | | | | | | | | |
| 2016  | | | | | | | | | | |
| 3     | 10           | ↑         | 5     | 5 | -135.9 | 0     | 0.70  | 2.5 | 54.6        | 0.04 |
| Null  |              |           | 4     | 4 | -141.0 | 8.1   | 0.01  |     |     |
| 2017  | | | | | | | | | | |
| 8     |              | ↓         | ↑     | 8 | -251.6 | 0     | 0.29  | 1.3 | 9.6         | 0.02 |
| 5     |              | ↓         | 6     | 6 | -254.0 | 0.5   | 0.23  | 7.3 | 0.02       |
| 7     |              | ↑         | 7     | 7 | -253.0 | 0.6   | 0.22  | 7.2 | 0.02       |
| 2     |              | ↓         | 5     | 5 | -255.4 | 1.4   | 0.15  | 4.7 | 0.01       |
| 3     |              | ↓         | 5     | 5 | -256.5 | 3.6   | 0.05  |     |     |
| Null  |              |           | 4     | 4 | -258.0 | 4.6   | 0.03  |     |     |
| **F. nigra (N = 300)** | | | | | | | | | | |
| 2017  | | | | | | | | | | |
| 8     | 5            | ↑         | ↓     | 7 | -445.7 | 0     | 0.55  | 2.2 | 6.6 × 10³  | 0.03 |
| 6     | ↑            | ↓         | 6     | 6 | -447.5 | 1.6   | 0.25  | 4.2 | 3.0 × 10³  | 0.02 |
| 7     | ↑            | ↑         | 6     | 6 | -448.2 | 2.9   | 0.13  |     |     |
| 4     | ↓            |           | 5     | 5 | -450.0 | 4.5   | 0.06  |     |     |
| Null  |              |           | 3     | 3 | -458.7 | 17.7  | <0.001|     |     |

Notes: All model tree species for each emergence year are shown for those models with ΔAICc ≤ 10 that did not contain pretending variables, including confidence set models with ΔAICc < 2. Data structure for all species was a proportional binomial response, weighted with the number of seeds sown per pot. With the exception of the F. nigra data, when full datasets were used, inclusion of a zero-inflation factor greatly improved model fit (denoted by ZIB). Direction of treatment effects is shown. Predictor variable treatments are labeled as follows: XPred, small terrestrial herbivore exclusion; SubM, mixed canopy forest substrate; and %DecC, percent deciduous canopy cover. ΔAICc and AICcw weights (AICcw) are given, evidence ratios (ER) calculated for top model over second-ranked model and each model over the Null model (ER0), and pseudo-R² (McFadden 1973) calculated for each model. The number of observations in model sets (N) is indicated after the species name for 2016 and 2017, respectively, except for F. nigra (2017 only).
Fig. 4. Mean number of seedlings per pot with jittered points showing data spread for (a) *A. saccharum* 2016, (b) *B. alleghaniensis* 2016, (c) *T. occidentalis* 2016, (d) *A. saccharum* 2017, (e) *B. alleghaniensis* 2017, (f) *T. occidentalis* 2017, and (g) *F. nigra* 2017 emergence data. Total numbers of seedlings observed for each species in each emergence year are listed below each panel. Although these seedlings emerged in different years, panels (a–c, g) represent seeds that experienced the same herbivore exclusion treatments, whereas seeds represented in panels (d–f) were enclosed within the phase 2 herbivore exclosures.
explanatory models over Null models (pseudo-$R^2 < 0.04$; Tables 4 and 5). The total number of 
*A. saccharum* seedlings was nearly equivalent under mixed canopy ($n = 142$) and boreal 
canopy ($n = 122$) in 2016; however, 2017 emergence was greater under boreal ($n = 376$) than 
mixed ($n = 290$) canopy. Despite the presence of the canopy cover variable in the confidence set 
models for *F. nigra*, there appears to be little evidence of canopy composition influencing either 
*F. nigra* seedling presence or abundance, as the response values were essentially even between 
boreal (85 pots containing 204 seedlings) and mixed (98 pots containing 191 seedlings) stands 
(Fig. 5a).

**Substrate type**

The actual difference in emergence between the two substrates was small for all species, 
despite the substrate treatment being included in some of the top models (Tables 4 and 5). For 
example, when comparing the mean number of seedlings per seedling-containing pot (i.e., non-
zero data from abundance datasets) for the 2016 *B. alleghaniensis* and 2017 *F. nigra*, and *T. occidentalis* emergence data, the difference between mean number of seedlings in pots containing mixed forest substrate and boreal forest substrate was $0.6$ (mixed $= 2.22$, boreal $= 1.65$), $0.1$ (mixed $= 1.34$, boreal $= 1.23$), and $-0.5$ (mixed $= 1.90$, boreal $= 2.39$) seedlings, respectively.

Overall, substrate type was important in determining whether *F. nigra* seedlings would be pre-
sent and in what abundance in 2017, where *F. nigra* was negatively correlated with mixed forest 
substrate (Tables 4 and 5; Appendix S2: Tables S5, S6), contrary to substrate effects on 2016 *B. alleghaniensis* emergence and 2017 *T. occidentalis* emergence, which were positively associated with mixed forest substrate. Too few *T. occidentalis* emerged in 2016 ($n = 43$; Table 3) to include the substrate treatment in the model; however, over half of emerged seedlings occurred in mixed forest substrate treatment pots ($n = 26$).

**Microclimate**

We observed microclimatic variations across the island in 2017, including differences in the 
timing of the transition between spring and summer air temperature. Site 15A warmed up more 
quickly than its nearest neighboring sites, with mean May and June air temperatures being $2.4^\circ$ 
and $3.1^\circ$C warmer than 16f, and $1.3^\circ$ and $1.4^\circ$C warmer than its nearest neighbor, 16G (Fig. 1). 
Differences in microclimate between forest types within sites were generally small; in both May 
and June, boreal and mixed forest stands differed in mean air temperature by $0.1^\circ$C across all sites. 
Soils in mixed forest stands were observed to warm up slightly faster than soils in boreal stands, 
going from a mean $0.02^\circ$C ($SD = 2.53$) warmer in May to $0.4^\circ$C ($SD = 2.23$) warmer in June.

Of the *a priori* climate variables graphically explored using 2017 emergence data for each 
species, only a few relationships could be easily differentiated from possible site effects. 
*F. nigra* emergence revealed positive associations along an east–west gradient between the 
abundance of seedlings and over-winter soil moisture and temperature, spring soil moisture 
temperature, and spring air temperature; climate variables relevant to *F. nigra* emergence success (Figs. 1, 6). This trend is supported by the greatest emergence success of this species at the 15B site ($n = 102$), where unfortunately both HOBO sensor masts failed in February 2017. In contrast, emergence data for *A. saccharum*, *B. alleghaniensis*, and *T. occidentalis* did not appear well correlated with any of the three climate variables investigated (Fig. 7). For example, emergence of *A. saccharum* seedlings at 15D and 15C varied dramatically, despite similar climatic conditions leading up to the initial pulse of newly emerged seedlings in late May 2017 (Fig. 7a,d,g).

**DISCUSSION**

Our spatially extensive series of field experiments indicate that temperate tree species’ 
distributions are not limited by their ability to germinate beyond-range (in mature boreal 
stands) or at range edges (in mixed canopy forest stands), evidenced by successful seedling emergence across all experimental sites spanning insular Newfoundland. The ability of each species to successfully germinate beyond their current distibutional range provides indirect evidence that these species’ climatic niches extend well beyond their respective realized
niche space, at least for the demographic stages examined in this study. We have provided empirical evidence for each of our model species’ abilities to overcome early life-stage abiotic and biotic hurdles in environments beyond their current distribution. The seedling emergence patterns resulting from the two phases of our experiment, in many cases, supported our a priori predictions; large-seeded tree species were more vulnerable to seed predation, while small-seeded species were sensitive to canopy composition. Other findings, however, were unexpected, given what is known about these species’ germination requirements within their range boundaries. Of note, *F. nigra* was successful across all phase 1 experimental sites despite having a geographically constrained population on the island (Farar 1995) and the near-total lack of emergence success of *T. occidentalis*, given its geographic distribution on the mainland.

Fig. 5. Conditional density plots using 2017 emergence data to show the probability of finding (a) 0–5 *F. nigra*, (b) 0–10 *A. saccharum*, (c) 0–6 *B. alleghaniensis*, and (d) 0–3 *T. occidentalis* seedlings per pot under increasing deciduous canopy cover. Emergence data for *B. alleghaniensis* were adjusted for background contamination. Mean percent deciduous canopy composition values for blocks established in phase 1 (a) and phase 2 (b–d) are indicated. The negative association between deciduous canopy cover and *B. alleghaniensis* and *T. occidentalis* emergence is evident in panels (c) and (d), whereas no clear relationship appears for *F. nigra*. The majority of *A. saccharum* emergence took place at only two sites (15D and 16F), which had mean deciduous canopy compositions of 14% and 8% (boreal forest), and 74% and 72% (mixed forest), respectively.
Fig. 6. Conditional density plots showing probability of 1–5 \textit{F. nigra} seedlings occurring per pot in 2017 by (a) mean winter soil moisture, (b) mean winter soil temperature, and mean soil moisture (c), soil temperature (d), and air temperature (e) for the period of 19 May–17 June 2017, that is, during seedling emergence. Winter climate variables were averaged between first and last weeks with an average air temperature below 0\degree C (starts 28 November 2016 for all sites, ends 2 April 2017 for 15A and 15E, and 23 April 2017 for all other sites). Mean values for climate variables at each site are indicated by the position of the sites above each panel. Total number of seedlings observed at each site is also given below site names.
A striking finding was the apparent lack of importance in the role our measured climatic drivers played in the model species’ emergence patterns. *F. nigra* emergence was weakly correlated with climatic variables, as expected from well-known species-specific germination requirements. Within its mainland range, *F. nigra* is commonly found in boggy, water-saturated sites (Gates 1942, Wright and Rauscher 1990) and, as expected, the site at which *F. nigra* emergence was poorest (15E) was the driest and coolest site for the 30-day period leading up to the initial emergence of seedlings.
pulse of newly emerged seedlings in mid-June 2017, and had the lowest mean over-winter soil moisture. Contrary to known within-range climatic drivers, B. alleghaniensis emergence was highest in cooler sites during spring 2017. In fact, most (93%) of the B. alleghaniensis seedlings observed in 2017 occurred at sites with mean temperatures much colder than previously determined optimal germination temperatures (20°–23°C; Perala and Alm 1990), suggesting other factors were dominant in driving emergence of this species. Though these findings are based on only a single year of climate data, three of the model species had emergence numbers in 2016 comparable to those in 2017 (Table 3), suggesting that our observations are repeatable.

Our analyses of 2017 emergence data with climate variables (Figs. 6, 7), paired with the overall emergence results, appear to confirm that regions of Newfoundland are within the climatic envelope of the BTE species tested here. Yet, despite the stage apparently being set for colonization of the island by a larger suite of temperate tree species than naturally dispersed here (MacPherson 1995), their widespread establishment has not occurred (Pastor and Mladenoff (MacPherson 1995), their widespread establishment has not occurred (Pastor and Mladenoff 1995), suggesting other factors were dominant in driving emergence of this species. Though these findings are based on only a single year of climate data, three of the model species had emergence numbers in 2016 comparable to those in 2017 (Table 3), suggesting that our observations are repeatable.

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**Canopy–seedbed interactions**

The delay in spring canopy closure in sites with greater dominance of deciduous species, rather than conifer-dominated canopies, may have benefitted B. alleghaniensis and F. nigra emergence, both positively associated with increasingly deciduous canopy, due to the integral role light exposure plays in breaking seed dormancy (Yelenosky 1961). We observed small increases in spring soil temperatures in mixed forest stands compared to boreal forest stands, suggesting that more solar radiation was reaching the forest floor due to increased canopy openness before spring leaf flush of deciduous trees (Lieffers et al. 1999). Yet, the benefits of increased spring light transmission on B. alleghaniensis emergence appear to have been outweighed in the 2017 germination year by the competing smothering effects of leaf litter. This negative smothering effect was absent in 2016 uncaged pots, likely due to the change in cage design. The phase 1 closed-top cage designs prevented leaf litter from reaching the ground within the cages, therefore eliminating any potential smothering effect that could have occurred.

Contrary to our predictions, our substrate manipulation treatment revealed that leaf litter occurring under a mixed canopy was not a significant barrier to B. alleghaniensis or T. occidentalis emergence; we found no evidence supporting any correlation between B. alleghaniensis emergence and a specific substrate type and, surprisingly, found a positive association between T. occidentalis emergence and mixed forest substrate in 2017. The relative success of these species on a predominantly leaf litter substrate, which has poor moisture-bearing capacity (Linteau 1948, Buda et al. 2011), may be partially explained by the mixed forest stand composition, specifically the low density of established maples, which shed leaves that tend to mat and create a hard, dry barrier for the small seedlings (Burton et al. 1969), at any of the experimental sites. Alternatively, while the moisture-retaining qualities of leaf litter are poor, early summer in southern Newfoundland is characterized by an average 81–104 mm of precipitation and relatively cool temperatures (Environment and Climate Change Canada 2017), perhaps reducing the risk of seedling desiccation. Regardless, the conditions under which T. occidentalis seedlings emerged most successfully in 2017—on leaf litter substrate under predominantly boreal canopy—are rare under natural conditions, and this poses questions about whether range expansion throughout Newfoundland is likely.

In line with what others have found, A. saccharum emergence was unaffected by substrate (Barras and Kellman 1998, Kellman 2004). In contrast, Caspersen and Saprunoff (2005) found that A. saccharum recruitment was significantly limited on leaf litter substrate compared to a greater variety of substrates than the number included in our study; however, here we investigated a direct comparison between leaf litter and moss substrates, whereas they did not. There
was also little evidence that *A. saccharum* suffered from any potential smothering effect, when the effects of both substrate type and canopy composition are considered together. One potential reason for this may again be attributable to the greater prevalence of birch species, which shed leaves that tend to curl rather than form a mat compared to maple leaves (Burton et al. 1969).

*A. saccharum* is a shade-tolerant species (Godman et al. 1990) and, as expected, emergence was greatest under 80–95% canopy cover in both years. While there appears to be limited literature discussing the effects of canopy composition on *A. saccharum* seedling emergence, a study by Reinhart et al. (2012) suggested that seedling recruitment of *A. saccharum* was greater near heterospecific individuals than conspecifics. *A. saccharum* had notably greater emergence success at sites with mean May air temperatures within the ideal range for *A. saccharum* germination (16F and 15D; Solarik et al. 2016). A difference in mean May air temperatures of less than 1°C separated these sites from others with far lower success rates (15C and 16H), and emergence at warmer sites was less than 2% (Fig. 7g).

The importance of deep organic layers is well established within *F. nigra*’s natural distribution (Gucker 2005). The moisture retention properties of soils with deep organic layers of partially decomposed moss (Turetsky et al. 2012) may explain our finding of *F. nigra*’s preferential emergence on mossy substrates that are characteristic of the boreal forest stands. Despite increased emergence on mossy substrates, *F. nigra*’s emergence was not correlated with canopy composition, likely due to the similarity in both growing season and winter soil moisture conditions between boreal and mixed forest stands (Fig 5a). *F. nigra* also appeared uninhibited by increasing canopy cover; the likelihood of 100% emergence in a pot in 2017 was greatest in pots with 70–80% total canopy cover.

**Vertebrate predation constrains large-seeded tree establishment**

*A. saccharum* emergence was well explained by protection from terrestrial vertebrate herbivory in both study years. This followed our expectations that *A. saccharum* would be targeted by terrestrial vertebrate granivores looking for larger, more food-rich seeds than typical boreal forest propagules; a phenomenon that has been observed within (Hsia and Francl 2009) and at the edge (Brown and Vellend 2014) of its native distribution in mainland North America. The large size of *A. saccharum* seeds and seedlings also made it easy to observe damage, which was often consistent with invertebrate herbivory patterns (Nystrand and Granström 2000, Meiners and Handel 2000).

Protection from herbivory also increased *F. nigra* success, although to a lesser extent than for *A. saccharum*. To the best of our knowledge, this is the first study to directly examine the effects of post-dispersal seed predation on *F. nigra*’s reproductive success either within its range or at its range edge. Based on work done with other species with similar seed sizes (De Steven 1991, Hulme and Hunt 1999) and the long period in situ prior to germination, we predicted that *F. nigra* would be vulnerable to seed predation. Our assumption was borne out, insofar as our analysis pointed to the herbivory treatment as being among the most important of the treatment variables; however, the effect size overall was limited. Unlike *A. saccharum* emergence in 2017, *F. nigra* emergence was more consistent across sites (Table 2); however, while both species experienced greater emergence success within exclosures at most sites (in either year for *A. saccharum*), this was not ubiquitous and both species experienced greater success outside of exclosures at select sites. We hypothesize that the site-specific predation effects were likely driven by variability in predator abundance across the study region.

We propose that the differential strength of seedling herbivory effects on *F. nigra* and *A. saccharum* was likely driven by differences in the timing of their respective germination. *A. saccharum* emergence occurred in May, before much of the forest floor herb layer had emerged (personal observations; well-documented germination strategy, Godman et al. 1990, Solarik et al. 2016), and we hypothesize that their seedlings were the first new growth to attract the attention of herbivores. *F. nigra* seedlings emerged in June, after the forest floor herb layer had flushed out. This problematic early-bird phenology for *A. saccharum* may persist as rising spring temperatures across Newfoundland (Natural Resources...
Canada 2015) are likely to induce a phenological shift to earlier emergence of both forest herb layer species and *A. saccharum* (Walther et al. 2002). Tree–insect herbivore systems are tightly linked (Schwartzberg et al. 2014), and phenological synchrony between the herbivorous species feeding on *A. saccharum* seedlings and their emergence period will likely continue despite potential changes in emergence phenology. Within its native range, *A. saccharum* can overcome the seed and seedling herbivory bottleneck through well-synchronized masting years, where a pulse of seedlings survives the early life-stage herbivory filter through herbivore satiation (Schnurr et al. 2002). The masting strategy may not be as effective in range edge or marginal site populations, where lower adult tree density will likely prevent seed and seedling herbivory pressures to be satiated, even if masting events do occur.

Contrary to our predictions, the herbivory treatment effect was evident for the small-seeded temperate species in both emergence years, even though these species’ seeds are not readily differentiable in size from those of typical boreal tree species (Bartlett et al. 1991, Bonner and Karrfalt 2008). While post-dispersal seed predation on *B. alleghaniensis* and *T. occidentalis* has been observed in their native ranges (Kelly et al. 2001, Larouche et al. 2011), here, the importance of the herbivore exclusion treatment effect observed in *T. occidentalis* and *B. alleghaniensis*’ 2016 emergence data may have indirectly been due to protection from smothering (discussed above), rather than, or in combination with, protection from herbivory. Alternatively, the variability in the importance of the herbivory treatment between the emergence years might reflect inter-annual variation in naturally occurring seed production, inter-annual variation in the invertebrate seed predator population (Korpimäki and Krebs 1996), or some other unmeasured variable.

**Further research**

Some elements of our study limited our ability to offer predictions of how emergence of temperate tree species might be controlled by specific drivers across Newfoundland. Our two emergence years’ datasets would have been more comparable, for example, had the experimental design remained consistent; however, it would have been irresponsible to not apply valuable methodological lessons gleaned from phase 1 to phase 2. While the low emergence rates do represent challenges to the inferential power of any analysis we performed, this is not uncommon in field-based manipulative germination experiments (De Steven 1991, Ronnenberg et al. 2008), especially when adding seed beyond their natural distribution range (Brown and Vellend 2014).

Since the primary focus of our study was to further generate research on the topic of temperate tree range expansion, there are many questions that easily spring from our findings. We would initially pose the question of whether terrestrial vertebrate predators are the only limiting herbivory-related factor, or whether invertebrate herbivores pose a greater barrier to successful germination for temperate tree species in Newfoundland, as they do in other areas (Pigot and Leather 2008). Notable here was the prevalence of slugs within test pots; Nystrand and Granström (2000) found that slugs were the most important seedling herbivores in their boreal Swedish study area. Evidence that damage and mortality of newly emerged seedlings were caused by slugs, such as the physical presence of slugs in test pots and slime trails near seedlings, was consistent with that described by Nystrand and Granström (1997) and slugs may pose a serious establishment barrier for introduced and native tree species alike (Moss and Hermanutz 2010). Seed and seedling herbivory were prevalent across all sites, species, and during both germination years, which have made it abundantly clear that further experimentation with these species to differentiate the effect of different herbivore groups is necessary. From our results, we would expect the herbivore group responsible for posing the greatest barrier to germination would change, depending on seed size and germination phenology.

Our results may also prompt questions related to assisted migration. We have demonstrated strong biotic constraints on temperate tree range expansion under ongoing climate change, even when tree seed is artificially planted in climatically favorable sites. A natural subsequent question, both ecologically and philosophically, is then: Is there a role for assisted migration in the northern expansion of temperate tree species? Will these biotic constraints simply cause a time
lag until temperate species are able to recruit beyond their range (e.g., once enough seed is produced and dispersed to satiate predators), or is this an example of a system where individuals will need to be transplanted for northward expansion? While we have no answer to that here, these are pertinent questions in a time of intense, ongoing climate change at northern range edges across North America that warrant further consideration.

CONCLUSIONS

We have shown that for all species, but particularly for species with large seeds relative to the native flora, seed predation poses an effective barrier to seedling emergence across Newfoundland. It is apparent that there are sufficient substrate types for germination to occur in mature forested stands of varying compositional complexities in Newfoundland, but that further work needs to be done to investigate substrate and soil qualities in relation to canopy composition to identify linkages between the aboveground and belowground nutrient flows (Wardle et al. 2004) and, in turn, their effect on seedling emergence, survival, and growth. Finally, while climatic variables did not appear well correlated with emergence success of most of our model species, these may become more important at later life-stages, such as promoting growth rates adequate to escape moose herbivory (McInnes et al. 1992) and adequate GDD for healthy seed production (Sykes et al. 1996). Further research investigating these and other temperate tree species’ survival, growth, and transition between crucial life-stages is needed to understand how isolated boreal forest systems may become colonized by southern tree species with a changing climate.

ACKNOWLEDGMENTS

This research was conducted on the ancestral homelands of the Beothuk and Mi’kmaq peoples. Research funding was provided by Research and Development Corporation of Newfoundland and Labrador, a Natural Sciences and Engineering Research Council Undergraduate Student Research Award and Canada Graduate Student Masters award, and Memorial University of Newfoundland. We would like to thank Shawn Leroux and Evan Edinger for discussion and advice throughout the project, Yolanda Wiersma and Anthony Taylor for critical review of an earlier draft of this manuscript, Lucas Brehaut for map production, as well as Rebecca Smyth, Margie Wilkes, Louis Charron, Jen Sullivan, Emily Wells, Willem Peters, Rachel Smith, and Chelsea Bloom for assistance with (grueling) fieldwork and sample analyses in the laboratory. PE and CDB designed the study; PE and ALC initiated the experiments and collected the data; PE led the data analyses and writing with contributions from ALC and CDB.

LITERATURE CITED

Agriculture and Agri-Food Canada. 2000. Plant hardiness zones of Canada geospatial platform viewer. http://www.agr.gc.ca/atlas/agpv?webmap-en=7852970071d4cabb13e99404ef10&webmap-fr=c1b54842d37480bb080747817d34c2
Agriculture and Agri-Food Canada, and Government of Canada. 2019. Agroclimate interactive maps. http://www.agr.gc.ca/atlas/agclimate
Ahti, T., L. Hämet-Ahti, and J. Jalas. 1968. Vegetation zones and their sections in northwestern Europe. Annales Botanici Fennici 5:169–211.
Aitken, S. N., S. Yeaman, J. A. Holliday, T. Wang, and S. Curtis-McLane. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications 1:95–111.
Akaike, H. 1998. Information theory and an extension of the maximum likelihood principle. Pages 199–213 in Selected papers of Hirotugu Akaike. Springer, New York, New York, USA.
Anderson, D. R. 2007. Model based inference in the life sciences: A primer on evidence. Springer Science & Business Media, New York, New York, USA.
Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike’s information criterion. Journal of Wildlife Management 74:1175–1178.
Arris, L. L., and P. S. Eagleson. 1989. Evidence of a physiological basis for the boreal-deciduous forest ecotone in North America. Vegetatio 82:55–58.
Barras, N., and M. Kellman. 1998. The supply of regeneration micro-sites and segregation of tree species in a hardwood/boreal forest transition zone. Journal of Biogeography 25:871–881.
Bartlett, R. M., R. J. Reader, and D. W. Larson. 1991. Multiple controls of cliff-edge distribution patterns of Thuja occidentalis and Acer saccharum at the stage of seedling recruitment. Journal of Ecology 79:183–197.
Bigelow, S. W., and C. D. Canham. 2015. Litterfall as a niche construction process in a northern hardwood forest. Ecosphere 6:art117.
Bolker, B., and R Core Team. 2016. bbmle: Tools for General Maximum Likelihood Estimation. https://CRAN.R-project.org/package=bbmle_

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S.- S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24:127–135.

Bonner, F. T. 1990. Storage of seeds: potential and limitations for germplasm conservation. Forest Ecology and Management 35:35–43.

Bonner, F. T., and R. P. Karrfalt, editors. 2008. The woody plant seed manual. United States Department of Agriculture, Forest Service, Washington, D.C., USA.

Brooker, R. W., J. M. J. Travis, E. J. Clark, and C. Dytham. 2007. Modelling species’ range shifts in a changing climate: the impacts of biotic interactions, dispersal distance and the rate of climate change. Journal of Theoretical Biology 245:59–65.

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Maechler, and B. M. Bolker. 2017. Modeling Zero-Inflated Count Data With glmmTMB.

Brown, C. D., and M. Vellend. 2014. Non-climatic constraints on upper elevational plant range expansion under climate change. Proceedings of the Royal Society B: Biological Sciences 281:20141779.

Buda, N. J., R. G. White, G. J. Kayahara, S. F. Duckett, and B. E. Fox. 2011. Silvicultural practices for eastern white cedar in boreal Ontario. 51 Pages. Technical Report, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.

Burnham, K. P., and D. R. Anderson. 2003. Model selection and multimodel inference: A practical information-theoretic approach. Springer Science & Business Media, New York, New York, USA.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods & Research 33:261–304.

Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65:23–35.

Burns, R. M., and B. H. Honkala, editors. 1990. Silvics of North America: 1. conifers; 2. hardwoods. United States Department of Agriculture, Forest Service, Washington, D.C., USA.

Burton, D. H., H. W. Anderson, and L. F. Riley. 1969. Natural regeneration of yellow birch in Canada. Pages 55–73 in Doolittle, W. T., and P. E. Bruns, comps. 1969. Birch symposium proceedings; 1969 August 19–21; Durham, NH. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Upper Darby, Pennsylvania, USA.

Cade, B. S. 2015. Model averaging and muddled multimodel inferences. Ecology 96:2370–2382.

Caspersen, J. P., and M. Saprunoff. 2005. Seedling recruitment in a northern temperate forest: the relative importance of supply and establishment limitation. Canadian Journal of Forest Research 35:978–989.

Chambers, D., C. Périé, N. Casajas, and S. de Blois. 2013. Challenges in modelling the abundance of 105 tree species in eastern North America using climate, edaphic, and topographic variables. Forest Ecology and Management 291:20–29.

Comes, H. P., and J. W. Kadereit. 1998. The effect of Quaternary climatic changes on plant distribution and evolution. Trends in Plant Science 3:432–438.

Cornett, M. W., P. B. Reich, K. J. Puettmann, and L. E. Frelich. 2000. Seedbed and moisture availability determine safe sites for early Thuja occidentalis (Cupressaceae) regeneration. American Journal of Botany 87:1807–1814.

Côté, M., J. Ferron, and R. Gagnon. 2003. Impact of seed and seedling predation by small rodents on early regeneration establishment of black spruce. Canadian Journal of Forest Research 33:2362–2371.

Damman, A. W. H. 1983. An ecological subdivision of the Island of Newfoundland. Pages 163–206 in R. South, editor. Biogeography and ecology of the Island of Newfoundland. Springer Science & Business Media, New York, New York, USA.

Davis, M. B., and R. G. Shaw. 2001. Range shifts and adaptive responses to quaternary climate change. Science 292:673–679.

De Steven, D. 1991. Experiments on mechanisms of tree establishment in old-field succession: seedling emergence. Ecology 72:1066–1075.

Donohue, K., L. Dorn, C. Griffith, E. Kim, A. Aguilera, C. R. Polisetty, J. Schmitt, and L. Galloway. 2005. Environmental and genetic influences on the germination of arabidopsis thaliana in the field. Evolution 59:740–757.

Elder, B. D. 2003. The impact of changing flow regimes on riparian vegetation and the riparian species Mimulus guttatus. Ecological Applications 13:1610–1625.

Elderd, B. D. 2003. The impact of changing flow regimes on riparian vegetation and the riparian species Mimulus guttatus. Ecological Applications 13:1610–1625.

Environment and Climate Change Canada. 2017. Canadian Climate Normals. http://climate.weather.gc.ca/climate_normals/

Environmental Design and Management Ltd. 2006. St. John’s urban forest master plan. 70 Pages. Environmental Design and Management Ltd, St, John’s, Newfoundland, Canada.
Evans, P., and C. D. Brown. 2017. The boreal–temperate forest ecotone response to climate change. Environmental Reviews 25:423–431.

Evans, P., E. L. Davis, Z. Gedalof, and C. D. Brown. 2018. Small herbivore exclusion cages alter micro-climate conditions. Forest Ecology and Management 415–416:118–128.

Farrar, J. L. 1995. Trees in Canada. Fitzhenry and Whiteside, Ottawa, Ontario, Canada.

Figueroed, F. O. G., G. Zuquim, H. Tuomisto, G. M. Moulatlet, H. Balslev, and F. R. C. Costa. 2018. Beyond climate control on species range: the importance of soil data to predict distribution of Amazonian plant species. Journal of Biogeography 45:190–200.

Finnis, J. 2013. Projected impacts of climate change for the province of Newfoundland and Labrador. 134 Pages. Memorial University of Newfoundland, St. John’s, Newfoundland, Canada.

Forestry and Agrifoods Agency. 2015. Tree Species. http://www.faa.gov.nl.ca/forestry/our_forest/tree_species/index.html

Freedman, D. A. 1983. A note on screening regression equations. American Statistician 37:152–155.

Galipaud, M., M. A. F. Gillingham, M. David, and F.-X. Dechaume-Moncharmont. 2014. Ecologists overestimate the importance of predictor variables in model averaging: a plea for cautious interpretations. Methods in Ecology and Evolution 5:983–991.

Gates, F. C. 1942. The bogs of northern lower Michigan. Ecological Monographs 12:214–254.

Godman, R. M., H. W. Yawney, and C. H. Tubbs. 1990. Acer saccharum Marsh., sugar maple. Pages 78–91 in R. M. Burns and B. H. Honkala, editors. Silvics of North America. U.S. Department of Agriculture, Forest Service, Washington, D.C., USA.

Goldblum, D., and L. S. Rigg. 2010. The deciduous forest – boreal forest ecotone. Geography Compass 4:701–717.

Gucker, C. L. 2005. Fraxinus nigra. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Fort Collins, CO, USA.

Hargreaves, A. L., K. E. Samis, and C. G. Eckert. 2014. Are species’ range limits simply niche limits writ large? A review of transplant experiments beyond the range. American Naturalist 182:157–173.

Harsch, M. A., P. E. Hulme, M. S. McGlone, and R. P. Duncan. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecology Letters 12:1040–1049.

Hegland, S. J., A. Nielsen, A. Lázaro, A.-L. Bjerknes, and Ø. Totland. 2009. How does climate warming affect plant-pollinator interactions? Ecology Letters 12:184–195.

Hsia, J. F., and K. E. Francl 2009. Postdispersal sugar maple (Acer saccharum) seed predation by small mammals in a northern hardwood forest. The American Midland Naturalist 162:213–223.

HilleRisLambers, J., M. A. Harsch, A. K. Ettinger, K. R. Ford, and E. J. Theobald. 2013. How will biotic interactions influence climate change–induced range shifts? Annals of the New York Academy of Sciences 1297:112–125.

Howe, H. F., J. S. Brown, and B. Zorn-Arnold. 2002. A rodent plague on prairie diversity. Ecology Letters 5:30–36.

Hulme, P. E., and M. K. Hunt. 1999. Rodent post-dispersal seed predation in deciduous woodland: predator response to absolute and relative abundance of prey. Journal of Animal Ecology 68:417–428.

Hup, C. M., and C. H. Yansa. 2009. Late Holocene vegetation history of the forest tension zone in central lower Michigan, USA. Physical Geography 30:205–235.

Hurvich, C. M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297–307.

Iverson, L. R., and A. M. Prasad. 2002. Potential redistribution of tree species habitat under five climate change scenarios in the eastern US. Forest Ecology and Management 155:205–222.

Kawecki, T. J., and D. Ebert. 2004. Conceptual issues in local adaptation. Ecology Letters 7:1225–1241.

Kellman, M. 2004. Sugar maple (Acer saccharum Marsh.) establishment in boreal forest: results of a transplantation experiment. Journal of Biogeography 31:1513–1522.

Kelly, D., D. E. Hart, and R. B. Allen. 2001. Evaluating the wind pollination benefits of mast seeding. Ecology 82:117–126.

Korpimäki, E., and C. J. Krebs. 1996. Predation and population cycles of small mammals. BioScience 46:754–764.

Kottke, M., J. Grieser, C. Beck, B. Rudolf, and F. Rubel. 2006. World map of the Köppen-Geiger climate classification updated. Meteorologische Zeitschrift 15:259–263.

Lafleur, B., D. Parè, A. D. Munson, and Y. Bergeron. 2010. Response of northeastern North American forests to climate change: Will soil conditions constrain tree species migration? Environmental Reviews 18:279–289.

Larouche, C., J.-C. Ruel, and J.-M. Lussier. 2011. Factors affecting northern white-cedar (Thuja occidentalis) seedling establishment and early growth in
mixedwood stands. Canadian Journal of Forest Research 41:568–582.
Leflers, V. J., C. Messier, K. J. Stadt, F. Gendron, and P. G. Comeau. 1999. Predicting and managing light in the understory of boreal forests. Canadian Journal of Forest Research 29:796–811.
Linteau, A. 1948. Factors affecting germination and early survival of yellow birch (Betula lutea Michx.) in Quebec. The Forestry Chronicle 24:27–86.
Logan, J. A., J. Regniere, and J. A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. Frontiers in Ecology and Environment 1:130–137.
MacPherson, J. B. 1995. A 6 ka BP Reconstruction for the Island of Newfoundland from a synthesis of Holocene lake-sediment pollen records. Géographie Physique Et Quaternaire, Géographie Physique Et Quaternaire 49:163–182.
Magnusson, A., H. J. Skaug, A. Nielsen, C. W. Berg, K. Kristensen, M. Maechler, K. J. van Bentham, B. M. Bolker, and M. E. Brooks. 2017. glmmTMB: Generalized Linear Mixed Models using Template Model Builder. https://github.com/glmmTMB
McCarragher, S., D. Goldblum, and L. Rigg. 2011. Geographic variation of germination, growth, and mortality in Sugar Maple (Acer saccharum): common garden and reciprocal dispersal experiments. Physical Geography 32:1–21.
McFadden, D. L. 1973. Conditional logit analysis of qualitative choice behavior. Pages 105–142 in Frontiers in Econometrics. Wiley, New York, New York, USA.
McInnes, P. F., R. J. Naiman, J. Pastor, and Y. Cohen. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. Ecology 73:2059–2075.
McKenney, D. W., J. H. Pedlar, K. Lawrence, K. Campbell, and M. F. Hutchinson. 2007. Potential impacts of climate change on the distribution of northern American trees. BioScience 57:939–948.
Meiners, S. J., and S. N. Handel. 2000. Additive and nonadditive effects of herbivory and competition on tree seedling mortality, growth, and allocation. American Journal of Botany 87:1821–1826.
Moss, M., and L. Hermanutz. 2010. Monitoring the small and slimy—protected areas should be monitoring native and non-native slugs (Mollusca: Gastropoda). Natural Areas Journal 30:322–327.
Munier, A., L. Hermanutz, J. D. Jacobs, and K. Lewis. 2010. The interacting effects of temperature, ground disturbance, and herbivory on seedling establishment: implications for treeline advance with climate warming. Plant Ecology 210:19–30.
Murtaugh, P. A. 2007. Simplicity and complexity in ecological data analysis. Ecology 88:56–62.
Natural Resources Canada. 2015. Climate and climate-related trends and projections. http://www.nrcan.gc.ca/environment/resources/publications/impacts-adaptation/reports/assessments/2008/10261
Nystrand, O., and A. Granström. 1997. Forest floor moisture controls predator activity on juvenile seedlings of Pinus sylvestris. Canadian Journal of Forest Research 27:1746–1752.
Nystrand, O., and A. Granström. 2000. Predation on Pinus sylvestris seeds and juvenile seedlings in Swedish boreal forest in relation to stand disturbance by logging. Journal of Applied Ecology 37:449–463.
Olson, D. M., et al. 2001. Terrestrial ecoregions of the world: a new map of life on earth. BioScience 51:933–938.
Parmesan, C., and M. E. Hanley. 2015. Plants and climate change: complexities and surprises. Annals of Botany 116:849–864.
Pastor, J. 2016. What should a clever moose eat? natural history, ecology, and the north woods. Island Press, Washington, D.C., USA.
Pastor, J., and D. J. Mladenoff. 1992. The southern boreal-northern hardwood forest border. Pages 216–240 in H. H. Shugart, R. Leemans and G. B. Bonan, editors. A systems analysis of the global boreal forest. Cambridge University Press, Cambridge, UK.
Perala, D. A., and A. A. Alm. 1990. Potential impacts of climate change: implications for treeline advance. Forest Ecology and Management 274.
Pielou, E. C. 1991. After the ice age: The return of life to glaciated north America. University of Chicago Press, Chicago, Illinois, USA.
Pigot, A. L., and S. R. Leather. 2008. Invertebrate predators drive distance-dependent patterns of seedling mortality in a temperate tree Acer pseudo-platanus. Oikos 117:521–530.
Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, R. Core, and R Core Team. 2017. nlme: Linear and nonlinear mixed effects models. https://CRAN.R-project.org/package=nlme
Putnam, R. C., and P. B. Reich. 2017. Climate and competition affect growth and survival of transplanted sugar maple seedlings along a 1700-km gradient. Ecological Monographs 87:130–157.
R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Reinhart, K. O., D. Johnson, and K. Clay. 2012. Effects of trees on their recruits in the southern Appalachians, USA. Forest Ecology and Management 263:268–274.
Rocca, M. E., P. M. Brown, L. H. MacDonald, and C. M. Carrico. 2014. Climate change impacts on fire regimes and key ecosystem services in Rocky
Mountain forests. Forest Ecology and Management 327:290–305.

Ronnemberg, K., K. Wesche, and I. Hensen. 2008. Germination ecology of Central Asian Stipa spp: differences among species, seed provenances, and the importance of field studies. Plant Ecology 196:269–280.

Schnurr, J. L., R. S. Ostfeld, and C. D. Canham. 2002. Direct and indirect effects of masting on rodent populations and tree seed survival. Oikos 96:402–410.

Schwartzberg, E. G., M. A. Jamieson, K. F. Raffa, P. B. Reich, R. A. Montgomery, and R. L. Lindroth. 2014. Simulated climate warming alters phenological synchrony between an outbreak insect herbivore and host trees. Oecologia 175:1041–1049.

Solarik, K. A., D. Gravel, A. Ameztegui, Y. Bergeron, and C. Messier 2016. Assessing tree germination resilience to global warming: a manipulative experiment using sugar maple (Acer saccharum). Seed Science Research 26:153–164.

Solarik, K. A., C. Messier, R. Ouimet, Y. Bergeron, and D. Gravel. 2018. Local adaptation of trees at the range margins impacts range shifts in the face of climate change. Global Ecology and Biogeography 27:1507–1519.

Svenning, J.-C., and F. Skov. 2005. The relative roles of environment and history as controls of tree species composition and richness in Europe. Journal of Biogeography 32:1019–1033.

Svenning, J.-C., and F. Skov. 2007. Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? Ecology Letters 10:453–460.

Sykes, M. T., I. C. Prentice, and W. Cramer. 1996. A bioclimatic model for the potential distributions of north European tree species under present and future climates. Journal of Biogeography 23:203–233.

Symonds, M. R. E., and A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike’s information criterion. Behavioral Ecology and Sociobiology 65:13–21.

Thomsen, M. S., T. Wernberg, A. Altieri, F. Tuya, D. Guldbrandsen, K. J. McGlathery, M. Holmer, and B. R. Silfman. 2010. Habitat cascades: the conceptual context and global relevance of facilitation cascades via habitat formation and modification. Integrative and Comparative Biology 50:158–175.

Tsuyuzaki, S., K. Narita, Y. Sawada, and K. Kushida. 2014. The establishment patterns of tree seedlings are determined immediately after wildfire in a black spruce (Picea mariana) forest. Plant Ecology 215:327–337.

Turetsky, M. R., B. Bond-Lamberty, E. Euskirchen, J. Talbot, S. Frolking, A. D. McGuire, and E.-S. Tunttila. 2012. The resilience and functional role of moss in boreal and arctic ecosystems. New Phytologist 196:49–67.

Ullah, M. I., and M. Aslam. 2017. mctest: Multicollinearity Diagnostic Measures. https://CRAN.R-project.org/package=mctest

Urban, M. C., L. D. Meester, M. Vellend, R. Stoks, and J. Vanoverbeke. 2012. A crucial step toward realism: responses to climate change from an evolving metacommunity perspective. Evolutionary Applications 5:154–167.

Urban, M. C., P. L. Zarnetske, and D. K. Skelly. 2013. Moving forward: dispersal and species interactions determine biotic responses to climate change. Annals of the New York Academy of Sciences 1297:44–60.

Vanstone, D. E. 1974. Seed dormancy and after-ripening requirements of Fraxinus nigra Marsh. Master of Science, University of Manitoba, Winnipeg, Manitoba, Canada.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389–395.

Wardle, D. A., R. D. Bardgett, J. N. Kilonomos, H. Setlå, W. H. van der Putten, and D. H. Wall. 2004. Ecological linkages between aboveground and belowground biota. Science 304:1629–1633.

Westman, W. E. 1978. Measuring the inertia and resilience of ecosystems. BioScience 28:705–710.

Wright, J. W., and H. M. Rauscher. 1990. Fraxinus nigra Marsh., Black Ash. InBurns, R. M., and B. H. Honkala, editors. Silvics of North America. U.S. Department of Agriculture, Forest Service, Washington, D.C., USA.

Yawney, H. W., and M. C. Jr Clayton. 1968. Sugar maple seed research. Pages 115–123 in Proceedings. USDA Forest Service, Northeastern Area State and Private Forestry, Upper Darby, Pennsylvania, USA.

Yelenosky, G. 1961. Birch seeds will germinate under a water-light treatment without pre-chilling. Forest Research Note, Laconia Research Center, US Forest Service, Laconia, New Hampshire, USA.

Zarnetske, P. L., D. K. Skelly, and M. C. Urban. 2012. Biotic multipliers of climate change. Science 336:1516–1518.

Zhang, Z.-B., Z.-S. Xiao, and H.-J. Li. 2005. Impact of small rodents on tree seeds in temperate and subtropical forests, China. Pages 269–282 in Seed fate: predation, dispersal and seedling establishment. CABI Publ, Wallingford, Oxfordshire, UK.
Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, New York, USA.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3108/full