

Biotic filtering of northern temperate tree seedling emergence in beyond-range field experiments

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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.

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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 invaders to occupy (Westman 1978, Pielou 1991). Bigelow and Canham (2015) provide evidence for this in ecotonal 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 (Lafleur 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 south-eastern 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 ($T_{\text{base}} = 10^{\circ}\text{C}$), 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 Saprundoff 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

to tree seed and seedlings and (2) substrate, or seedbed composition under (3) boreal or mixed canopy composition forest type (see Appendix S2: Table S2 for stand composition data). Canopy composition and cover was visually estimated, using a spherical densiometer (Forest Densiometers, Rapid City, South Dakota, USA), to the species level during site establishment in phases 1 and 2 by averaging readings taken in each cardinal direction at each block (Appendix S2: Table S4). We defined boreal forest stands as having canopy composition that was a minimum of two-thirds (~66%) proportion of coniferous species, and mixed forest stands as having canopy composition of at least half (50%) deciduous species. We favored mixed stands containing canopy species commonly associated with the mainland North American BTE, such as white pine (*Pinus strobus* L.), yellow birch, black ash, and red maple (*Acer rubrum* L.), all of which are native to Newfoundland (Farrar 1995, Forestry and Agrifoods Agency 2015). Mixed stands were further required to have predominantly broadleaf-litter dominated substrate (rather than needle leaf litter) and <30% moss substrate cover, whereas boreal forest stands were required to have >60% moss substrates cover. Determinations of substrate composition were estimated visually within each 2 × 2 m planting block. Here, substrate refers to the top of the organic layer (i.e., the seedbed) and soil represents the organic and mineral components below that.

During phase 1, five sites were established across southern Newfoundland (47°10' N–49°21' N and 53°23' W–58°15' W; Fig. 1; Appendix S2: Table S2). These five sites were duplicated, and a further three sites ($n = 8$) were established in phase 2 (2016; Fig. 1). We added sites during the second phase of the experiment due to the high mortality rates all species experienced during phase 1. Site establishment, which involved experimental treatment setup and seedling, took place between 12 and 19 September 2015 (phase 1) and 15 and 22 October 2016 (phase 2). Five planting blocks were established in each boreal and mixed forest stand at each study site (Fig. 2), for a total of 10 blocks per site. We employed a full factorial experimental design, for both experimental phases, manipulating substrate, and herbivore exclusion under each forest type, such that each block had pots of

each treatment for each species under each forest type, with half of those pots occurring under exclusion cages (Fig. 2). Seedling surveys generally took 1–2 days per site and were conducted over the 2016 and 2017 growing seasons. Seedling emergence count data were collected in May and September 2016 (phase 1) and monthly from mid-May to mid-September 2017 (phases 1 and 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 re-inserted 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

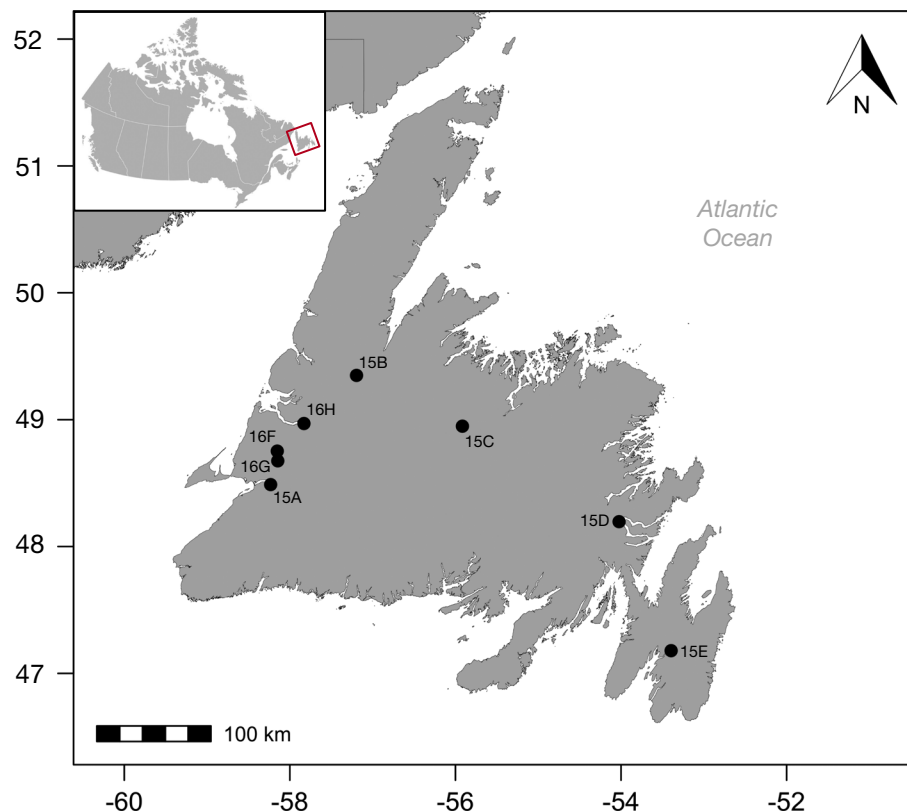


Fig. 1. Study site locations across the island of Newfoundland. 15E, 15D, 15C, 15B, and 15A were established in 2015 (phase 1), and 16F, 16G, and 16H, in addition to the original five sites established during phase 1, were used in phase 2. Sites established in 2016 for phase 2 were concentrated in the island's southwest, which has the highest tree canopy species diversity of any region in the province (Farrar 1995).

enclosure cage designs that have been used (Coté 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 enclosure 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 enclosure 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

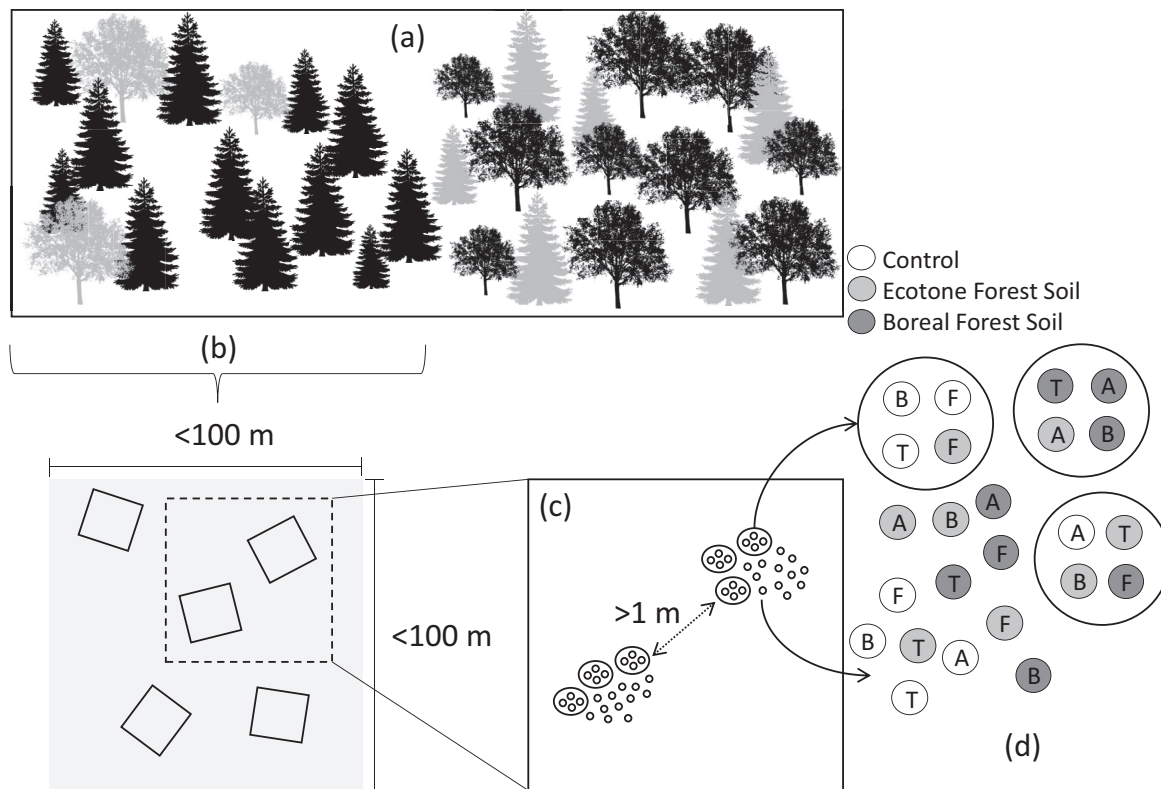


Fig. 2. Experimental design diagram showing (a) conceptualized difference in canopy composition between boreal and ecotone forest types (left and right, respectively) and (b) planting block layout shown within one of the two forest types within each site. Blocks are approximately 2 × 2 m in dimension, 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*.

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 × 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 × 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

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 $\times$ 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 (ZIB) 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 $\Delta\text{AICc} \leq 2$ to have essentially as much explanatory power as the top-ranked model (i.e.,

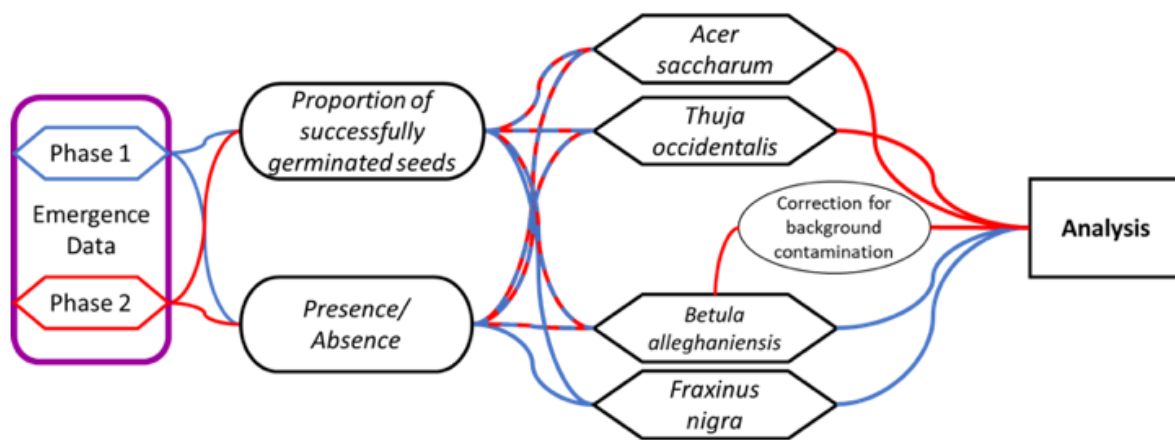


Fig. 3. Emergence data for each phase of the experiment were analyzed separately. Seedling emergence was recorded as both (1) a Bernoulli presence/absence response (presence data) and (2) a binomial proportion response, which was the number of seedlings that emerged in a pot out of the total number of seeds that could have germinated (abundance data). The number of naturally occurring *Betula* sp. seedlings counted during the 2017 (phase 2) growing season at each block was divided by the total number of pots not sown with *B. alleghaniensis* seeds within each block ($n = 18$). The resulting value was rounded up to the nearest integer and subtracted from each pot seeded with *B. alleghaniensis* to correct for background contamination within the corresponding block (Elder 2003, Donohue et al. 2005).

$\Delta\text{AICc} = 0$), models with a ΔAICc between 4 and 7 are considerably weaker, and models with $\Delta\text{AICc} > 7$ 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), glmmTMB (Magnusson et al. 2017, Brooks et al. 2017), and bbmle (Bolker and R Core Team 2016). Pseudo- R^2 values for binomial models were calculated after McFadden (1973). A confidence set of best-supported models was created for each combination of species $\times$ response variable for each emergence year and was populated by fitted models with a $\Delta\text{AICc} < 2$. We removed models containing

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.

pretending variables (sensu Anderson 2007), or uninformative parameters (sensu Arnold 2010) from our confidence sets (Appendix S2: Tables S5 and S6). Models containing variables with parameter estimates that reached zero within 1 standard error were considered uninformative and were omitted from the confidence set. This process of confidence set creation is also found in the analytical methodology of those employing AIC weights to perform model averaging (Burnham et al. 2011, Symonds and Moussalli 2011); however, we did not use model averaging, as the weaknesses of this practice have been well described by others (e.g., Galipaud et al. 2014, Cade 2015). Also, our primary objective was to provide evidence-based descriptive analyses to serve as a baseline for future hypothesis generation, rather than predictive models. Presenting a set of top models provides more information of possible mechanistic relationships for future investigation.

Using 2017 emergence datasets for each model species, climate variables of known importance were graphically assessed. Conditional density plots were generated from the raw presence and abundance data, using the graphics package in R, to explore whether important within-range relationships between climate variables and seedling emergence were also important in our novel beyond-range system. This procedure was chosen over attempting to model the data, as our

climate data were too coarse to differentiate specific climate drivers from possible site effects.

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

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	16F	16G	16H
<i>A. saccharum</i>	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
<i>B. alleghaniensis</i>	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
<i>F. nigra</i>	...	...	...	...	...	41.0	34.0	23.0	25.7	8.0	...	...	...
<i>T. occidentalis</i>	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			
	Presence		Abundance		Presence		Abundance	
	%	N	%	N	%	N	%	N
<i>A. saccharum</i>	29.0	600	8.8	3000	25.0	480	13.9	4,800
<i>B. alleghaniensis</i>	28.0	300	5.4	3000	10.4	480	2.0	4,800
<i>F. nigra</i>	...	...	...	...	61.0	300	26.3	1,500
<i>T. occidentalis</i>	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.

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 $\times$ 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

Table 4. Model results for treatment variable analysis of presence data.

Model	Predictor			k	LogL	ΔAICc	AICcw	ER	ER_0	R^2
	XPred	SubM	%DecC							
<i>A. saccharum</i> ($N = 588, 480$)										
2016										
3	↑			4	−270.0	0	0.45	1.1	4.8×10^{19}	0.15
5	↑		↑	5	−269.1	0.2	0.39		4.3×10^{19}	0.15
6	↑	↑		6	−269.6	3.2	0.09			
8	↑	↑	↑	7	−268.8	3.7	0.07			
Null				3	−316.4	90.7	<0.001			
2017										
3	↑			4	−140.2	0	0.41	1.7	2.9	0.01
Null				3	−142.2	2.1	0.15			
<i>B. alleghaniensis</i> ($N = 293, 480$)										
2016										
3	↑			4	−152.8	6.3	0.031	2.7	731.4	0.05
Null				3	−160.5	19.5	<0.001			
2017										
2			↓	4	−222.9	0	0.46	1.1	280.5	0.03
5	↑		↓	5	−221.9	0.2	0.42		258.8	0.03
Null				3	−229.6	11.3	0.002			
<i>T. occidentalis</i> ($N = 588, 480$)										
2016										
3	↑			4	−111.9	0	0.71	2.6	89.6	0.05
Null				3	−117.4	9.0				
2017										
2			↓	4	−202.9	0	0.31	1.3	3.6	0.01
5	↓		↓	5	−202.2	0.6	0.23		2.7	0.01
7		↑	↓	6	−201.5	1.3	0.16		1.9	0.02
8	↓	↑	↓	7	−200.8	1.8	0.12		1.4	0.02
Null				3	−205.3	2.6	0.08			
<i>F. nigra</i> ($N = 300$)										
2017										
8	↑	↓	↑	7	−176.0	0	0.27	1.3	5.0	0.03
5	↑		↑	5	−178.4	0.5	0.21		3.9	0.02
3	↑			4	−179.7	1.2	0.15		2.8	0.01
6	↑	↓		6	−177.9	1.7	0.12		2.2	0.02
7		↓	↑	6	−178.2	2.2	0.09			
2			↑	4	−180.5	2.6	0.07			
Null				3	−181.8	3.3	0.05			

Notes: All model tree species for each emergence year are shown for those models with $\Delta\text{AICc} \leq 10$ that did not contain pre-tending variables, including confidence set models with $\Delta\text{AICc} < 2$. Data structure for all species was a Bernoulli response, and models were binomial with a logit link function. 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 AICc weights (AICcw) are given, evidence ratios (ER) calculated for top model over second-ranked model and each model over the Null model (ER_0), and pseudo- R^2 (McFadden 1973) is calculated for each model. The Model column refers to the models shown in Table 1. 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).

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 ($n = 106$

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

Model	Model weight	Predictor			k	LogL	ΔAICc	AICcw	ER	ER_0	R^2
		XPred	SubM	%DecC							
<i>A. saccharum</i> (ZIB; $N = 588, 480$)											
2016											
3	5	↑			5	−452.8	0	0.42	1.2	9.4×10^{19}	0.06
5		↑		↑	6	−452.0	0.4	0.34		7.7×10^{19}	0.10
6		↑	↑		7	−451.8	2.1	0.14			
8		↑	↑	↑	8	−451.2	2.9	0.10			
Null					4	−499.8	92.1	<0.001			
2017											
5	10	↑		↓	6	−417.5	0	0.64	3.0	1.1×10^4	0.02
2				↓	5	−419.7	2.2	0.21			
Null					4	−426.6	14.0	<0.001			
<i>B. alleghaniensis</i> (ZIB; $N = 293, 480$)											
2016											
6	10	↑	↑		7	−240.6	0	0.71	2.5	2.4×10^6	0.07
Null					4	−258.5	29.5	<0.001			
2017											
5	10	↑		↓	6	−353.6	0	0.49	1.7	647.6	0.02
2				↓	5	−355.2	1.1	0.29		377.7	0.02
Null					4	−362.2	13.0	<0.001			
<i>T. occidentalis</i> (ZIB; $N = 588, 480$)											
2016											
3	10	↑			5	−135.9	0	0.70	2.5	54.6	0.04
Null					4	−141.0	8.1	0.01			
2017											
8		↓	↑	↓	8	−251.6	0	0.29	1.3	9.6	0.02
5		↓		↓	6	−254.0	0.5	0.23		7.3	0.02
7			↑	↓	7	−253.0	0.6	0.22		7.2	0.02
2				↓	5	−255.4	1.4	0.15		4.7	0.01
3		↓			5	−256.5	3.6	0.05			
Null					4	−258.0	4.6	0.03			
<i>F. nigra</i> ($N = 300$)											
2017											
8	5	↑	↓	↑	7	−445.7	0	0.55	2.2	6.6×10^3	0.03
6		↑	↓		6	−447.5	1.6	0.25		3.0×10^3	0.02
7			↓	↑	6	−448.2	2.9	0.13			
4			↓		5	−450.0	4.5	0.06			
Null					3	−458.7	17.7	<0.001			

Notes: All model tree species for each emergence year are shown for those models with $\Delta\text{AICc} \leq 10$ that did not contain pre-tending variables, including confidence set models with a $\Delta\text{AICc} < 2$. 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 AICc weights (AICcw) are given, evidence ratios (ER) calculated for top model over second-ranked model and each model over the Null model (ER_0), and pseudo- R^2 (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).

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

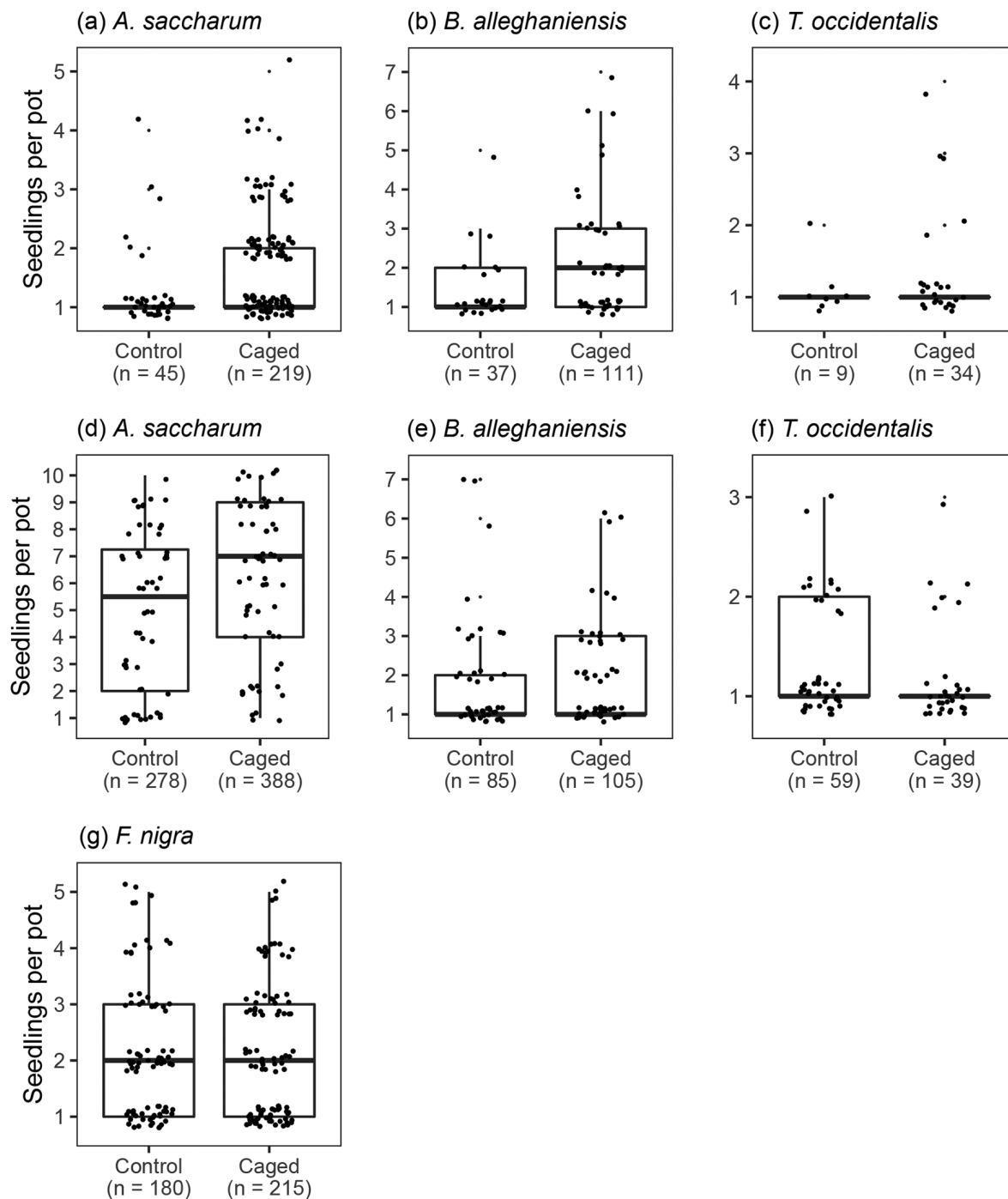


Fig. 4. Mean number of seedlings per pot with jittered points showing data spread for (a) *A. saccharum* 2016, (b) *B. alleghaniensis* 2016, (c) *T. occidentalis* 2016, (d) *A. saccharum* 2017, (e) *B. alleghaniensis* 2017, (f) *T. occidentalis* 2017, and (g) *F. nigra* 2017 emergence data. Total numbers 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 enclosures.

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 present 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° and 3.1°C warmer than 16F, and 1.3° and 1.4°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°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°C (SD = 2.53) warmer in May to 0.4°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 and 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 distributional range provides indirect evidence that these species' climatic niches extend well beyond their respective realized

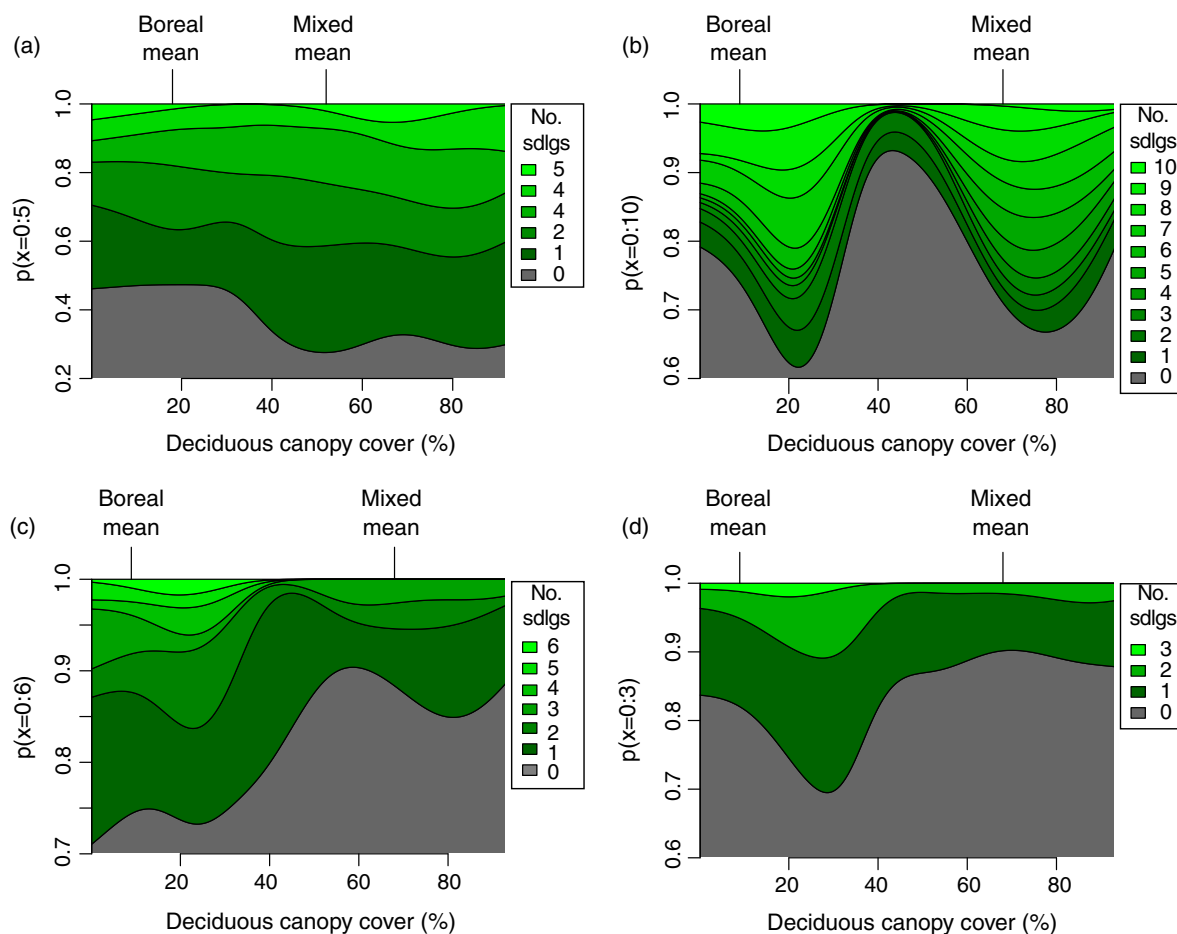


Fig. 5. Conditional density plots using 2017 emergence data to show the probability of finding (a) 0–5 *F. nigra*, (b) 0–10 *A. saccharum*, (c) 0–6 *B. alleghaniensis*, and (d) 0–3 *T. occidentalis* seedlings per pot under increasing deciduous canopy cover. Emergence data for *B. alleghaniensis* were 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.

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 (Farrar 1995) and the near-total lack of emergence success of *T. occidentalis*, given its geographic distribution on the mainland.

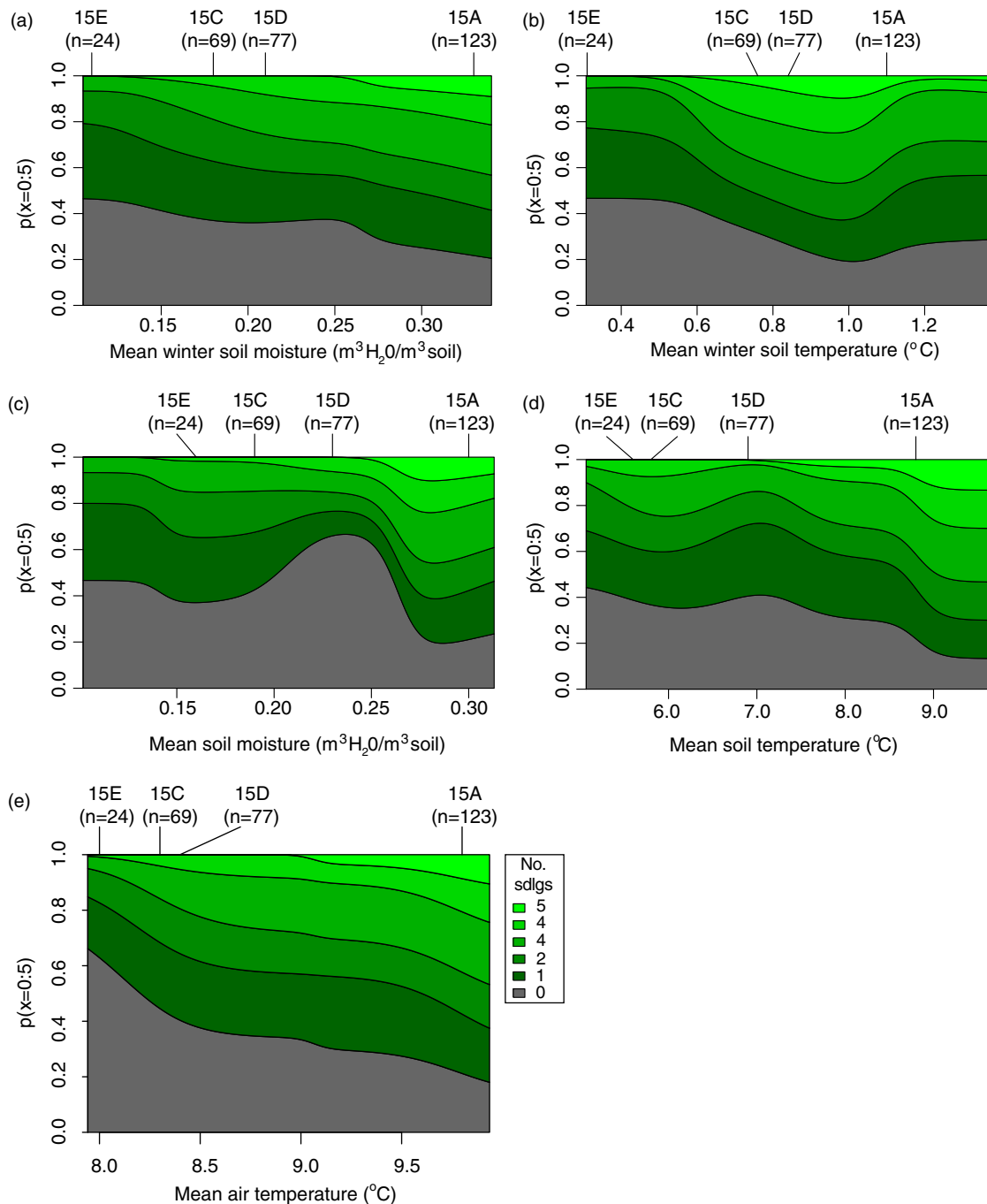


Fig. 6. Conditional density plots showing probability of 1–5 *F. nigra* seedlings occurring per pot in 2017 by (a) mean winter soil moisture, (b) mean winter soil temperature, (c) soil moisture, (d) soil temperature, and (e) air temperature for the period of 19 May–17 June 2017, that is, during seedling emergence. Winter climate variables were averaged between first and last weeks with an average air temperature below 0°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.

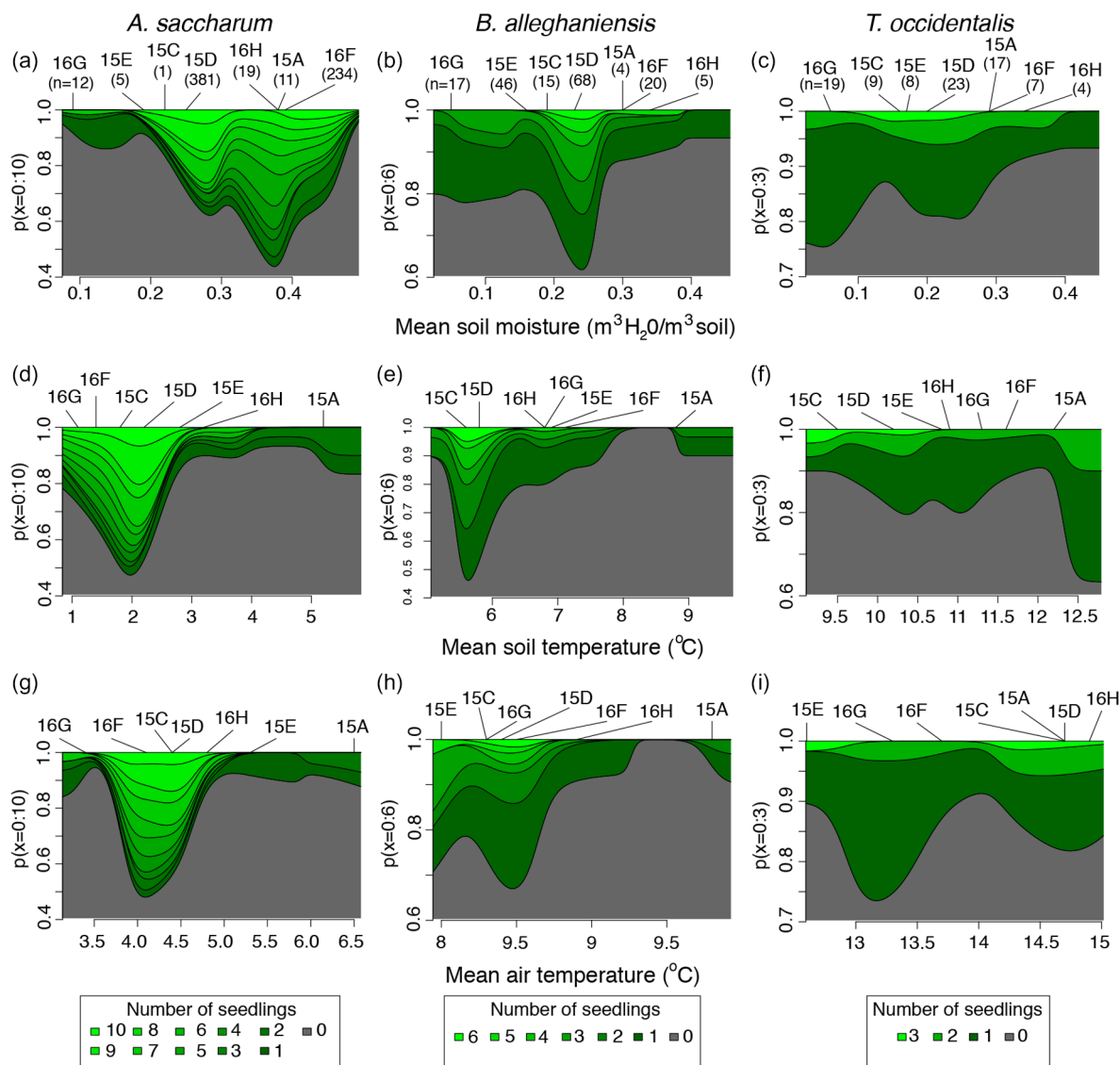


Fig. 7. Conditional density plots showing probability of 0–10 *A. saccharum* (a, d, g), 0–6 *B. alleghaniensis* (b, e, h), and 0–3 *T. occidentalis* (c, f, i) seedlings occurring per pot in 2017 by mean soil moisture (a, b, c), soil temperature (d, e, f), and air temperature (g, h, i). Periods from which means were taken are 24 April–23 May 2017 for *A. saccharum*, 19 May–17 June 2017 for *B. alleghaniensis*, and 11 June–10 July 2017 for *T. occidentalis*. 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 in first row.

Boreal–temperate ecotone and unfilled niche space

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

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 1992). Here, we have identified several current filters acting on the future expansion of temperate tree species- distributions into boreal forest stands on the island. These are acting independent of the dispersal barrier posed by the Cabot Strait, which for some mainland temperate tree species may be insurmountable without human intervention.

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 (Liefers 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 Franc 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.

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