



RESEARCH ARTICLE

Priority effects will impede range shifts of temperate tree species into the boreal forest

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Abstract

1. Temperate tree species are expected to expand their distribution into the boreal forest in response to climate change. However, it is becoming increasingly clear that many species will experience significant setbacks in capacity to migrate due to a series of unfavourable conditions impacting their recruitment success, and thus their ability to colonize new locations.
2. We quantify the relative influence of a series of factors important for tree seedling recruitment at range margins: propagule dispersal, substrate favourability and the influence of the local hetero-specific species canopy composition. We hypothesized that boreal trees are responsible for priority effects that influence the establishment of temperate tree species seedlings. To do so, we analysed two recruitment stages (first-year seedlings and older seedlings) for seven tree species: *Abies balsamea* (ABBA), *Acer rubrum* (ACRU), *Acer saccharum* (ACSA), *Betula papyrifera* (BEPA), *Betula alleghaniensis* (BEAL), *Populus tremuloides* (POTR) and *Fagus grandifolia* (FAGR) commonly found within the temperate-boreal ecotone forests of northeastern North America.
3. Overall, we found that boreal canopy trees influence the distribution of substrates, more specifically the occurrence of needle cover and decayed wood in recruitment plots. Interestingly, decayed wood was a poor substrate in almost all cases. This association between canopy and substrate led to highly unfavourable substrates that affected the seedling densities of all temperate tree species. In addition, we found that seedling dispersion was highly localized, where the mean dispersal distance of all trees occurred in close proximity of parent trees.
4. *Synthesis.* Unfavourable substrates and limited mean dispersal distance of trees due to resident boreal trees generate (strong) priority effects within the temperate-boreal ecotone. Together, these conditions promise to cause significant lags in temperate tree species migration into the boreal forest in the future.

KEYWORDS

boreal forest, climate change, ecotone, priority effects, recruitment, species migration, species range, temperate forest

1 | INTRODUCTION

Climate change has already begun to shift many geographical distributions of plants (Beckage et al., 2008; Gilliam, 2016; Kroiss & HilleRisLambers, 2015). As a result, novel community and species interactions should be expected with species colonization and extinction (Williams, Shuman, Webb, Bartlein, & Leduc, 2004; Woodall et al., 2013). The rate and magnitude of the projected changes will exceed the adaptive capacity of certain species (Aubin et al., 2016; Duputié, Rutschmann, Ronce, & Chuine, 2015; Iverson, Prasad, & Matthews, 2008; Kawecki & Ebert, 2004; Sexton, McIntyre, Angert, & Rice, 2009). Species lacking the ability to disperse fast enough and/or the plasticity to maintain their competitiveness under climate change will lag behind their optimal distribution, which could lead to significant declines in their abundance and promote extinctions (Aitken, Yeaman, Holliday, Wang, & Curtis-McLane, 2008; Solarik, Gravel, Ameztegui, Bergeron, & Messier, 2016; Solarik, Gravel, Ouimet, Bergeron, & Messier, 2018; Woodall et al., 2013).

Vulnerability to rapid changes in environmental conditions is particularly worrisome for trees because they are sessile organisms, long-lived, slow to reach reproductive maturity and typically have limited seed dispersal (Petit & Hampe, 2006; Lenoir & Svenning, 2013; but see Clark, 1998). Theory predicts that range expansion rates should scale with the mean dispersal distance (MDD) and the population growth rate in novel environments (Svenning et al., 2014). While we know much about dispersal kernels of forest trees (Greene, Canham, Coates, & LePage, 2004; Nathan, Klein, Robledo-Arnuncio, & Revilla, 2012), much less is known about population dynamics at range margins. Rapid changes in climate can significantly impact tree development, survival and phenology (Aitken et al., 2008; Gilliam, 2016; Vitasse et al., 2013; Walck, Hidayati, Dixon, Thompson, & Poschlod, 2011). Forest dynamics depend greatly on the regeneration stage, which is strongly influenced by the abiotic and biotic conditions occurring within the understory (De Frenne et al., 2013; Solarik et al., 2018). The regeneration stage is a key life-history event that involves several important and environmentally sensitive phases: flowering, pollination, seed maturation, propagule dispersal, seed germination, seedling establishment and subsequent survival (Fischelli, Frielich, & Reich, 2013; Kroiss & HilleRisLambers, 2015; Sexton et al., 2009; Solarik et al., 2016, 2018).

Species response(s) to climate change will lead to the contraction of some species' distributions while others will expand, together creating novel community assemblages (Gilliam, 2016; Hansen et al., 2001). These responses will likely be detectable first within the transition zone (ecotone), where species ranges currently overlap (Harper et al., 2005). Ecotones tend to have the highest environmental heterogeneity (Boulangeat, Gravel, & Thuiller, 2012; Solarik et al., 2018), are highly variable and under constant contraction and expansion (Gaston, 2009; Sexton et al., 2009). A species range limit is typically caused by a combination of some limitations in the species physiology to deal with environmental changes (i.e. northern ranges are too cold, southern ranges are too hot) and its interaction with the local biotic community (Godsoe, Jankowski, Holt, & Gravel,

2017); where even minor changes can cause significant reduction in competitiveness and impact the species ability to acquire resources (i.e. temperature, light, water, space; Beckage et al., 2008; Fischelli et al., 2013). Migrating tree species will likely face negative biotic interactions at the range limit, as they migrate towards novel habitats, where competitors are already established (HilleRisLambers, Harsch, Ettinger, Ford, & Theobald, 2013). Resident populations can further inhibit range shifts of invading species through priority effects (legacy effects). Such priority effects will occur when the resident lowers the availability of resources (e.g. light, space, nutrients) or changes the environment (e.g. soil pH) in a way giving it an advantage over invading species (Shulman et al., 1983; Urban & De Meester, 2009). These effects can be long-lasting, as they can persist long after a resident species has become maladapted to the local environment, further delaying invading species from colonizing—even if they are better adapted phenologically to the regional conditions (Atkins & Travis, 2010; Gilliam, 2016). They have been shown to occur within many ecosystems (Sexton et al., 2009) and can alter the association between the environment and species distribution (Leopold, Tanentzap, Lee, Heenan, & Fukami, 2014; Urban & De Meester, 2009).

Several factors have been proposed as key inhibitors of tree species range expansion: seed supply (fecundity) and dispersal are among the best studied (e.g. Clark, Lewis, McLachlan, & HilleRisLambers, 2003; Iverson et al., 2008) and typically seen as the primary cause for migration lags (Hargreaves, Samis, & Eckert, 2014; Sexton et al., 2009). The limited availability of seed within periphery populations is undoubtedly constrained by the abundance, proximity and fecundity of the parent trees in these populations (Aitken et al., 2008; Sexton et al., 2009). However, even when a seed source is present and able to disperse propagules at greater distances (≥ 100 m; Clark, 1998), unfavourable substrates could severely impact recruitment (Caspersen & Sapruff, 2005; Marx & Walters, 2008), especially for propagules travelling a greater distance from their parent (Kroiss & HilleRisLambers, 2015). The lack of suitable substrates for seedlings to first germinate and establish upon can have multiplicative effects, particularly at the range limit. More specifically, novel edaphic effects could arise, where the absence of key symbiotic microbial and fungal communities and/or nutrients (e.g. calcium and magnesium) could impact seedling emergence and survival (Collin, Kembel, Messier, & Bélanger, 2018; Lafleur, Paré, Munson, & Bergeron, 2010). Furthermore, as microclimate (i.e. light and temperature), competition and soil fertility within the understory are largely controlled by the overstorey canopy and its composition, the conditions occurring within the ecotone (i.e. species range overlap) could cause a mosaic of unfavourable recruitment sites altering the recruitment niche and demography (Benavides et al., 2016; Ibáñez et al., 2015; Reich et al., 2015; Solarik et al., 2018).

Our understanding of the factors controlling recruitment within the temperate-boreal ecotone remains limited, where few empirical studies have assessed the influence of non-climatic factors on regeneration dynamics at range margins (Brown & Vellend, 2014; HilleRisLambers et al., 2013). Although we have methods to

evaluate recruitment limitations caused by seed dispersal and microsite favourability (Clark, 1998), including response to forest management (Caspersen & Sapruff, 2005; LePage, Canham, Coates, & Bartemucci, 2000), rarely are they done at range limits within undisturbed canopies (but see Benavides et al., 2016; Drobyshev, Guitard, Asselin, Genries, & Bergeron, 2014). Our objective in this study is to test the hypothesis that priority effects are slowing recruitment of temperate tree species into the boreal forest. We do so by investigating the relative importance of a series of contributing factors known to influence tree seedling recruitment: seedling dispersal, fecundity and substrate favourability. We also consider the influence of local biotic neighbourhood, as a proxy of the potential effect of resident trees on unmeasured environmental variables. We predict that (a) the presence of boreal trees will diminish substrate quality within a stand for temperate trees, which will (b) cluster their spatial distribution and seedling density and (c) that the limited seedling dispersal capability of temperate tree species will magnify priority effects from boreal tree species.

2 | MATERIALS AND METHODS

2.1 | Study sites

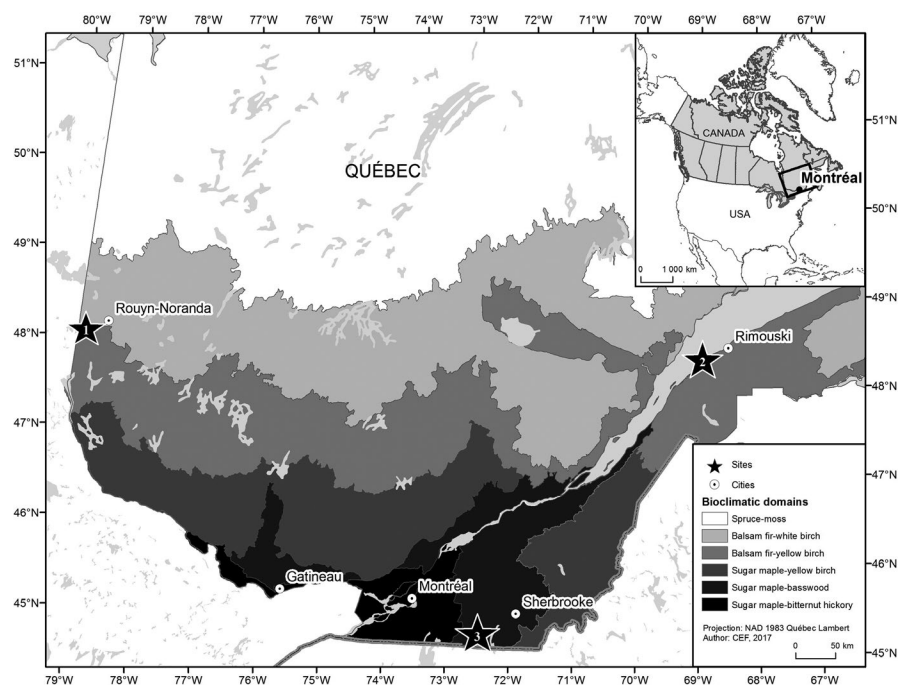
The study was conducted at three permanent sample sites established as part of the QUICCFOR network (QUantifying and mapping the Impact of Climate Change on FORest productivity of Eastern North America); (a) Abitibi-Temiscamisque (hereafter referred to as Abitibi) (48° 9'45.14"N, 79°24'4.39"W), (b) Le Bic (48°20'1.03"N, 68°49'3.79"W) and (c) Sutton (45° 6'46.09"N, 72°32'28.67"W) (Figure 1). All three sites are located within or at the limit of the northern temperate forest zone, where Abitibi is located within the balsam fir-white birch (*Abies balsamea*-*Betula papyrifera*) domain, Le

Bic within the balsam fir-yellow birch (*Betula alleghaniensis*) domain, while the Sutton site lies within the hardwood forest subzone, made up of the sugar maple-basswood (*Acer saccharum*-*Tilia Americana*) domain (Saucier, Grondin, Robitaille, & Bergeron, 2003). Elevation at the three sites ranged from 350 to 400 m in Abitibi, 200 to 320 m at Le Bic and 500 to 850 m at Sutton. The later drives a transition from primarily temperate dominated canopy species at the lower elevation (<650 m) to a balsam fir-yellow birch cover at a higher elevation. Mean annual temperature ranges among sites from -15.4°C in January to 19.7°C in July, whereas annual precipitation ranged from 868 to 1,314 mm (Environment Canada, 2019).

2.2 | Field sampling

A grid of 20 × 20 m quadrats were established at each site to map overstorey canopy trees. Each site varied in plot size, where the total area of mapped grids ranged from 200 to 320 m in width and 200 to 1,000 m in plot length. All trees within the study grid had their coordinates mapped using Leica Flexline© TS06 and TCR805 Total Stations. Each tree with a diameter at breast height (DBH) ≥10.0 cm was mapped, identified by species, given a health status (living, dead, declining, fallen) and its DBH (1.3 m) measured. In the late spring of 2015, four recruitment plots (1 m²) were established within each of the 20 × 20 m grids at a 5 × 5 m spacing (3,424 total recruitment plots across all three sites). Recruitment was measured as stem tallies by species over 2 years (2015 and 2016) for two recruitment stages: (a) first-year seedlings (referred to as stage 1 seedlings), identified by the presences of cotyledons, absence of terminal bud scars, suppleness of the stem and number of leaves; (b) older seedlings (referred to as stage 2 seedlings), which were not first year and were <30.0 cm in height. We visually estimated the per cent coverage (to the nearest 5%, total summing to 100%) of the recruitment plots by the following substrates:

FIGURE 1 Locations of the three (Abitibi-Temiscamisque, Le Bic and Sutton) QUICCFOR permanent long-term sample plots used in this study and their associated bioclimatic zones (Saucier et al., 2003)



grass, leaf, needles, moss, decayed logs (decay classes: 4–7, Mills & Macdonald, 2004), solid logs (decay classes: 1–3, Mills & Macdonald, 2004) and bole cover from overstorey/sapling trees. In addition to the substrates, we also assessed the cover of deciduous plant cover (non-canopy tree species) within the recruitment plot.

2.3 | Data analysis

2.3.1 | Ordination

We first performed a redundancy analysis (RDA) to investigate the association between substrate conditions and canopy composition. Essentially, an RDA is a canonical extension of a multiple regression that models multivariate response data (Y matrix: substrate type) in relation to an explanatory variable (X matrix: canopy tree basal area) (Legendre, Oksanen, & Braak, 2011). Prior to analysis, all response variables were standardized using the Hellinger Transformation, which reduces any extremely skewed values (Legendre & Gallagher, 2001). Statistical significance was assessed by comparing the initial *F*-statistic to the distribution of *F*-values obtained after 1,000 permutations of the response matrix and the goodness-of-fit evaluated with the adjusted R^2 (Peres-Neto, Legendre, Dray, & Borcard, 2006). All RDAs were done using the 'VEGAN' package in R (Oksanen et al., 2015).

2.3.2 | Seedling distribution model

Seedling distribution data were analysed using a modified version of the recruitment model first proposed by Ribbens, Silander, and Pacala (1994) and further developed by LePage et al. (2000), who added substrate favourability, and again by Caspersen and Sprunoff (2005) who added light availability. Due to the high degree of variability in measuring light availability in the understorey (Caspersen & Sprunoff, 2005); it was not directly measured in our models and instead it was approximated with the total basal area of neighbouring trees (Canham, Ruscoe, Wright, & Wilson, 2014). Below, we describe the model and processes included, then the modifications we implemented to construct the final model. We then describe our methodology for parameter estimation. We considered that the seedling produced by an individual parent tree *k*, follows a power function of the stem diameter of that tree (DBH_{*k*}):

Fecundity:

$$R_i = \text{STR} \left(\frac{\text{DBH}_k}{30} \right)^2, \quad (1)$$

where (R_i) is the number of recruits within a specific recruitment plot *i*. The total number of recruits (STR—standardized total recruits) is scaled to a parent tree with a DBH of 30.0 cm (Canham et al., 2014; LePage et al., 2000; Ribbens et al., 1994; Uriarte, Canham, Thompson, Zimmerman, & Brokaw, 2005). Typically, the power exponent is not estimated as it has been shown to covary with STR, and thus, we set it equal to 2 as in previous studies

(Caspersen & Sprunoff, 2005). We tested two alternative forms of commonly used isotropic dispersal kernels (Nathan et al., 2012). The first one being the exponential power dispersal kernel, with seed density declining monotonically with distance from the parent tree (LePage et al., 2000; Ribbens et al., 1994):

Dispersal (exponential power function):

$$g(d) = \frac{1}{K} e^{-(Bd)^\beta}, \quad (2a)$$

where *d* is the distance, *B* and β are estimated parameters, and *K* is a normalizer constant that ensures the probability will integrate to 1. Many previous studies have fixed β , however, some (Canham et al., 2014; Canham & Uriarte, 2006) allowed the parameter to vary, thus allowing the data to determine the appropriate shape, which we do here. The second dispersal kernel we tested was the lognormal, which has been shown to be more appropriate for both wind and animal-dispersed seeds (Greene et al., 2004):

Dispersal (lognormal):

$$g(d_k) = \frac{1}{K} e^{-1/2 \left(\frac{\ln\left(\frac{d}{X_O}\right)}{X_b} \right)^2}, \quad (2b)$$

where X_O is the median distance travelled, X_b determines the breadth or spread of the seed dispersal kernel, *d* is the distance from the centre of the recruitment plot to a parent tree and *K* is again a normalizer constant. Ribbens et al. (1994) combined Equations (1) and (2a) to calculate the expected number of recruits in a quadrat *i* by the summation of the contribution of all conspecific parent trees:

Fecundity and dispersal:

$$R_i = \text{STR} \sum_{k=1}^T \left(\frac{\text{DBH}_k}{30} \right)^2 g(d_k), \quad (3)$$

where R_i is the expected number of recruits in each recruitment plot *i* and *T* is the total number of parent trees in the mapped stand. LePage et al. (2000) first introduced substrate favourability into Equation (3) by weighting recruitment by the favourability of a particular substrate and its per cent cover within a recruitment plot:

Substrate favourability:

$$R_i = \sum_{j=1}^S (c_{ij} f_{ij}) \text{STR} \sum_{k=1}^T \left(\frac{\text{DBH}_k}{30} \right)^2 g(d_k), \quad (4)$$

where *S* is the total number of substrates, c_{ij} is the per cent cover of substrate *j* in recruitment plot *i* and f_{ij} is a parameter that quantifies the favourability of the given substrate. f_{ij} is constrained between 0 and 1; a value of 1 indicates that the density of seedlings in a given recruitment plot is limited by the size and proximity of parent trees and not the favourability of a certain substrate. On the contrary, a value of 0 indicates an unsuitable substrate and ultimately lowers

TABLE 1 Summary of models tested by the inclusion of contributing factors (zero-inflation, dispersal, substrate favourability and neighbourhood). The standardized total recruits (STR) is included in each model. The total number of models evaluated also includes the clipped and non-clipped versions of each of the models below, as well as the lognormal and exponential dispersal kernels

Model ID	Distribution (P_z)	Dispersal	Substrate Favourability (f)	Neighbourhood (P_b)
A (Null)	No	No	No	No
B	Yes	No	No	No
C	Yes	Yes	No	No
D	Yes	No	Yes	No
E	Yes	Yes	Yes	No
F	Yes	No	No	Yes
G	Yes	Yes	No	Yes
H	Yes	No	Yes	Yes
I	Yes	Yes	Yes	Yes
J	No	No	No	No
K	No	Yes	No	No
L	No	No	Yes	No
M	No	Yes	Yes	No
N	No	No	No	Yes
O	No	Yes	No	Yes
P	No	No	Yes	Yes
Q	No	Yes	Yes	Yes

seedling density. As our focus in this study was to evaluate seedling recruitment in the context of species migration, where biotic interaction(s) from surrounding canopy trees may become increasingly important and influence microsite conditions in a way that we cannot measure (e.g. if the presence of coniferous trees affecting snow accumulation and melting), we introduce the local neighbourhood effect from hetero-specific canopy trees. The effect of the local neighbourhood is accounted for by:

Neighbourhood effect:

$$R_i = \sum_{j=1}^S (c_{ij}f_{ij}) g(d_k) e^{-P_b \sum_{i=1}^B a_i} \text{STR} \sum_{k=1}^T \left(\frac{\text{DBH}_k}{30} \right)^2, \quad (5)$$

where B is the total number of hetero-specific canopy tree species within the local neighbourhood (≤ 20.0 m of recruitment plot centre), a_i is the total basal area of hetero-specific overstorey canopy trees within the neighbourhood and P_b is a parameter that quantifying the importance of the neighbourhood canopy—where a higher value of P_b indicates an unfavourable neighbourhood for recruitment, and thus lowers seedling density.

2.4 | Parameter estimation

We performed maximum likelihood estimation (MLE) of parameters Θ , which varies from one model to another (Table 1). As recommended by Canham et al. (2014), we assumed that the expected number of recruits follows a zero-inflated Poisson distribution, where P_z accounts for the larger than expected number of zero recruits presented in the recruitment plots. The likelihood of observation Y_i given parameters theta is therefore:

$$\text{Prob}(Y_i | \Theta) = \begin{cases} P_z + (1 - P_z) \text{Poisson}(0 | \Theta) & \text{if } Y_i = 0, \\ (1 - P_z) \text{Poisson}(Y_i | \Theta) & \text{if } Y_i > 0 \end{cases} \quad (6)$$

A large number of recruitment plots with zero seedlings can typically occur (e.g. Benavides et al., 2016) and consequently using a zero-inflated parameter avoids underestimating the total number of zeros found in the recruitment plots, as well as the overestimation of large count occurrences. We also tested models with P_z set to zero to ensure all possible model combinations were tested (Table 1). Our analysis was performed on the most common boreal; *Abies balsamea* - ABBA and *Betula papyrifera* - BEPA, and temperate; *Acer rubrum* - ACRU, *Acer saccharum* - ACSA, *Betula alleghaniensis* - BEAL, *Populus tremuloides* POTR, and *Fagus grandifolia* - FAGR canopy tree species present at each site, which together accounted for 69.9% (Abitibi), 84.4% (Le Bic) and 94.5% (Sutton) of the total overstorey canopy basal area. (Note: Only ABBA, ACSA and BEPA were present at all three sites.)

We estimated seedling density strictly for plots that were at least 20 m from the boundary of the mapped areas to avoid potential edge effects (Bin et al., 2011). We performed two separate dispersal analyses to evaluate the influence of long-distance dispersal: (a) a clipped analysis, where only parent trees within 20 m of the recruitment plot centre were used and (b) a non-clipped analysis, where all parent trees within the mapped permanent plot were included for dispersal kernel estimations. Finally, we set the substrate favourability of grass, solid logs, rock and canopy bole cover to 0 as they either had minimal coverage (<1%) within the recruitment plots overall or are inhibiting recruitment for obvious reasons, and thus were not

estimated in any of the analysis performed. The favourability for all other substrates was determined by the model, where substrates yielding an $f \geq 0.400$ were considered generally favourable, while an $f < 0.400$ were determined as unfavourable.

Maximum likelihood estimates were obtained with simulated annealing as the optimization algorithm. We used the numerical implementation of the latter provided in the GENSA package (Xiang, Gubian, Suomela, & Hoeng, 2013) of the statistical platform of R (R Development Core Team, 2019).

2.5 | Final model selection and confidence intervals

We first ran the null model (model A; Table 1), which was then tested against all possible model combinations (models B through Q; Table 1) for a given species, recruitment stage, site, clipped and non-clipped dispersal. The Akaike's Information Criterion (AIC) was computed, and models with the lowest AIC were assumed to be the 'most parsimonious'. The McFadden adjusted Pseudo R^2 (Seghieri, Do, Devineau, & Fournier, 2012) was also calculated against the null model to ensure the best final model selection. Confidence intervals were computed for each parameter by outputting the set of all estimates used in the annealing process, where on average it resulted in at least 100,000 sets of parameters for each model. We then excluded the sets of values which the log-likelihood exceeded the critical value of the χ^2 distribution ($\alpha = .05$ $df = 1$), where the minimum and maximum parameter values from the remaining sets (i.e. 95% confidence limits; see Caspersen & Sapruff, 2005). Below, we report the best models fit for each species, recruitment

stage and site combination regardless if it was a clipped or non-clipped model for both the 2015 and 2016 seedling density data.

3 | RESULTS

3.1 | Substrate distribution

Our RDA analysis supported our first prediction as we found an association between the distribution of boreal canopy trees (ABBA and BEPA) as averaged in the 20×20 m plots and the distribution of certain substrates (moss, decayed and/or needle), as averaged in four 1×1 m subplots, depending on the site (Figures 2, 3 and 4). The RDAs were all significant ($p \leq .001$), although they only explained between 3.2% (Le Bic, Figure 3) and 14.6% (Sutton, Figure 4) of the total variation in substrate distribution. While we assumed linear relationships as a first approximation, we found a positive association between temperate canopy trees (ACRU, ACSA and FAGR) and leaf coverage, and then another between boreal trees (ABBA and BEPA) with needle and decayed wood coverage (Figures 2, 3 and 4). These relationships were particularly apparent at the Sutton site, where an elevational gradient caused a more distinct separation in substrate cover and overstorey canopy composition (Figure 4).

3.2 | Model fit

Model fit differed across species, recruitment stages, sites and years, where the McFadden pseudo R^2 ranged from .032 to .733 (Table 2). Overall, the model fit was slightly higher at Le Bic (0.323) than either

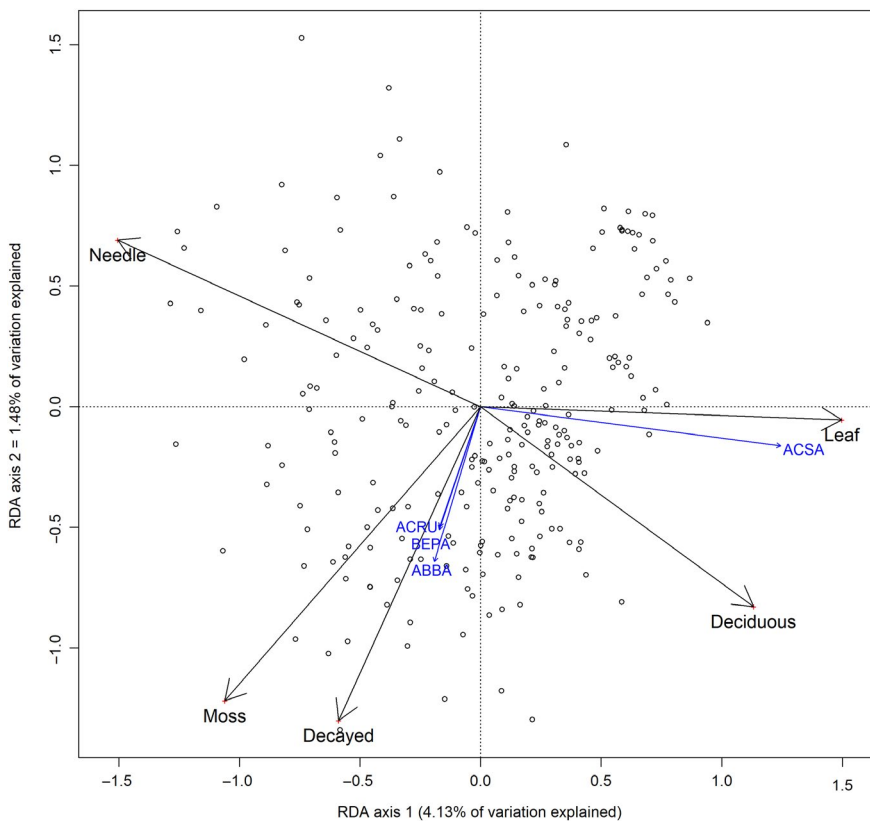


FIGURE 2 Redundancy analysis (RDA) for overstorey canopy basal area and substrate coverage at the Abitibi-Temiscaninque site. Circles indicate the recruitment plots while the crosses indicate the centroids of the response variables. Angles between the substrate and the arrows of the explanatory variables reflect their correlations, where arrow size is positively related to its effect level. If the projection of the substrate from the centre of the axis is parallel to the arrow of the explanatory variable, then they are considered related [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 3 Redundancy analysis (RDA) for overstorey canopy basal area and substrate coverage at the Le Bic site. Circles indicate the recruitment plots while the crosses indicate the centroids of the response variables. Angles between the substrate and the arrows of the explanatory variables reflect their correlations, where arrow size is positively related to its effect level. If the projection of the substrate from the centre of the axis is parallel to the arrow of the explanatory variable, then they are considered related [Colour figure can be viewed at wileyonlinelibrary.com]

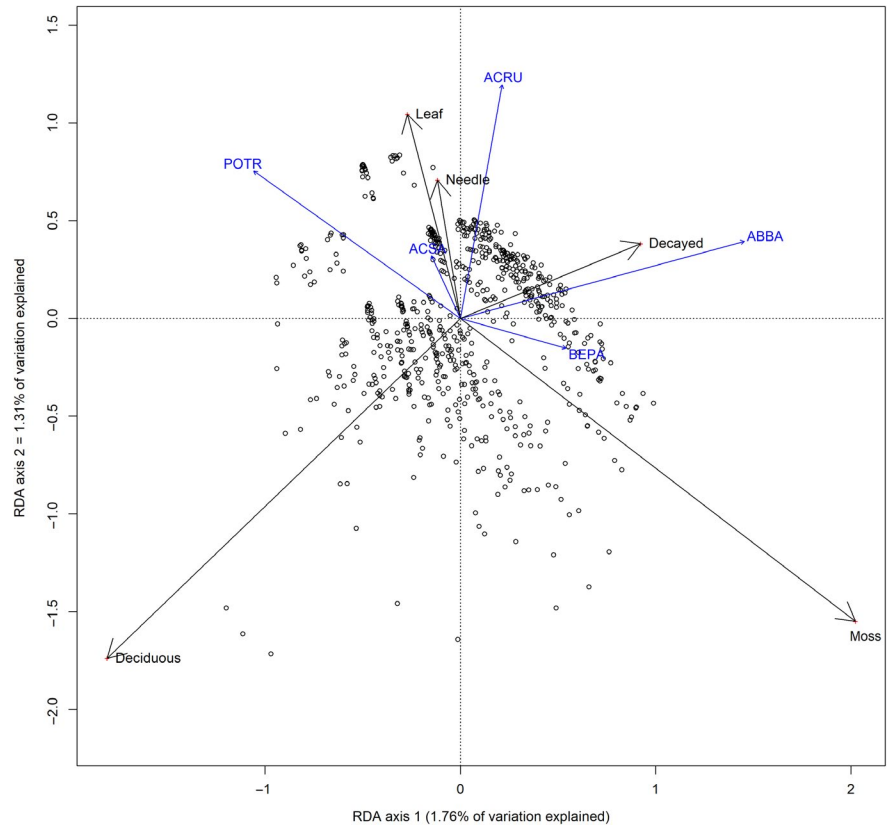
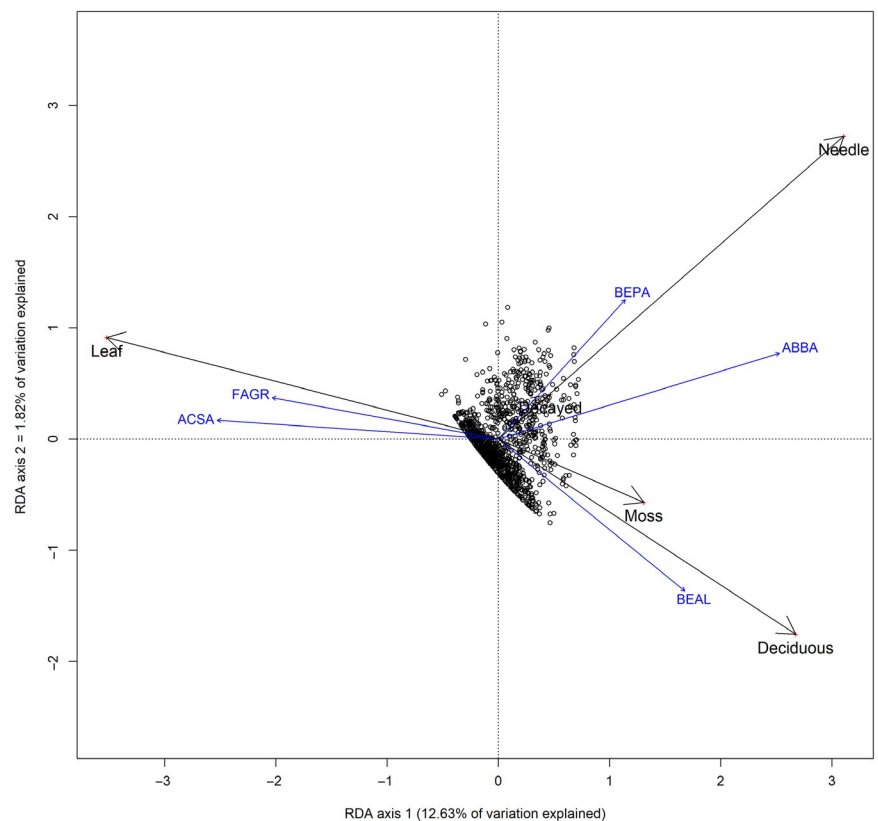


FIGURE 4 Redundancy analysis (RDA) for overstorey canopy basal area and substrate coverage at the Sutton site. Circles indicate the recruitment plots while the crosses indicate the centroids of the response variables. Angles between the substrate and the arrows of the explanatory variables reflect their correlations, where arrow size is positively related to its effect level. If the projection of the substrate from the centre of the axis is parallel to the arrow of the explanatory variable, then they are considered related [Colour figure can be viewed at wileyonlinelibrary.com]



the Abitibi (0.265) or Sutton (0.250) sites. Little change occurred in model fits between 2015 and 2016 at Abitibi (2015:0.252 and 2016:0.284) and Le Bic (2015:0.336 and 2016:0.309); however,

models from Sutton in 2016 explained only a third the variance in (0.121) compared to 2015 (0.379). These differences were found to be especially apparent when considering differences among

TABLE 2 Maximum likelihood estimates of the most parsimonious recruitment models by species, recruitment stage (Stage 1: first-year seedlings, Stage 2: older seedlings), year and site

Site	Abitibi		Le Bic				Sutton				
	2		1		2		1		2		
	2015	2016	2015	2016	2015	2016	2015	2016	2015	2016	
ABBA											
Model ID	I _{LC}	K _L	E _{LC}	G _E	C _{LC}	B	E _{LC}	E _L	NC	C _L	K _L
McFadden R ²	0.2660	0.3136	0.3362	0.2038	0.2971	0.0511	0.2859	0.1521		0.1188	0.0871
AIC	395.83	24.43	861.57	523.22	172.01	245.97	364.95	424.29		46.72	31.83
Zero-inflated	0.7285	0.8016	0.6438	0.6581	0.8868	0.7309	0.6695	0.5463		0.8896	NS
STR	4600.1	1.7	2535.3	614.0	64.5	0.6	1666.5	1014.8		586.9	37.5
MDD	9.72	13.7	10.5	23.8	18.2	NS	12.9	15.9		12.5	20.0
Dispersal	9.7/0.08	13.4/0.00	10.5/0.06	20.0/1.41	18.1/0.00	NS	12.9/0.01	14.9/0.37		11.6/0.40	20/0.04
Neighbourhood	0.4644	NS	NS	0.3433	NS	NS	NS	NS		NS	NS
ACRU											
Model	C _L	NC	D	B	H	E _E	D	C _L	Species Absent		
McFadden R ²	0.2723		0.2117	0.2648	0.3747	0.3706	0.4274	0.3047			
AIC	419.14		728.41	656.77	563.97	4446.16	273.44	255.76			
Zero-inflated	0.7351		0.5273	0.6619	0.7344	0.3787	0.8202	0.8570			
STR	435.3		12.0	2.8	83.7	22318.5	46.2	259.8			
MDD	22.7		NS	NS	NS	17.0	NS	8.2			
Dispersal	20.0/0.50		NS	NS	NS	15.2/1.51	NS	7.6/0.39			
Neighbourhood	NS		NS	NS	0.2053	NS	NS	NS			
ACSA											
Model	C _L	C _{LC}	E _L	C _L	D	E _L	D	D	H	E _L	E _L
McFadden R ²	0.3481	0.2959	0.3849	0.2959	0.5317	0.3759	0.1396	0.2268	0.4371	0.3906	0.4744
AIC	290.18	44.11	961.36	704.46	271.50	998.21	234.61	236.21	1044.17	375.03	532.21
Zero-inflated	0.7600	0.8742	0.4268	0.4241	0.8965	0.5210	0.7257	0.8393	0.5768	0.7914	0.7779
STR	190.6	33.7	2288.7	318.57	24.4	7592.3	17.0	13.8	298.1	1104.2	1847.2
MDD	18.3	14.1	22.5	21.6	NS	32.2	NS	NS	NS	104.9	20.1
Dispersal	16.2/0.49	14.1/0.01	20.0/0.48	20.0/0.40	NS	19.9/0.98	NS	NS	NS	19.9/1.82	19.9/0.10
Neighbourhood	NS	NS	NS	NS	NS	NS	NS	NS	0.5373	NS	NS

(Continues)

TABLE 2 (Continued)

Site	Abitibi		Le Bic		Sutton	
	1	2	1	2	1	2
Stage	2015	2016	2015	2016	2015	2016
Year	2015	2016	2015	2016	2015	2016
BEPA						
Model	C _{LC}	NC	NC	C _L	G _L	K _L
McFadden R ²	0.0865			0.3513	0.2745	0.4080
AIC	31.85	0.1112		112.08	96.80	27.25
Zero-inflated	0.5480	0.9106		0.9411	0.7731	NS
STR	1.2	0.7		521.9	1911.4	14.8
MDD	8.8	NS		19.7	15.0	43.1
Dispersal	8.7/0.04	NS		19.7/0.02	15.0/0.05	0.01/4.09
Neighbourhood	NS	NS		NS	1.0504	NS
BEAL						
Model	Species Absent		Species Absent		Z-F	Z-N
McFadden R ²					0.4203	0.1554
AIC					142.65	89.68
Zero-inflated					0.9286	0.7239
STR					42.1	1.1
MDD					NS	NS
Dispersal					NS	NS
Neighbourhood					NS	1.1479
POTR						
Model	Species Absent		NC		Species Absent	
McFadden R ²	K _{LC}		K _{LC}	C _{LC}	K _{LC}	
AIC	0.5260		0.5260	0.1668	0.5417	
Zero-inflated	17.49		17.49	108.37	8.00	
STR	NS		NS	0.8533	NS	
MDD	3.03		3.03	72.9	0.2	
Dispersal	7.0		7.0	10.8	6.9	
Neighbourhood	7.0/0.0		7.0/0.0	10.5/0.26	6.9/0.0	
	NS		NS	NS	NS	

(Continues)

TABLE 2 (Continued)

Site	Abitibi		Le Bic		Sutton	
	1	2	1	2	1	2
Stage	2015	2016	2015	2016	2015	2016
Year	2015	2016	2015	2016	2015	2016
FAGR						
Model	Species Absent	Species Absent	Species Absent	Species Absent	C _L	C _{LC}
McFadden R ²					0.2140	0.1381
AIC					380.12	115.55
Zero-inflated					0.6812	0.7776
STR					107.7	28.6
MDD					7.7	6.7
Dispersal					6.9/0.46	6.7/0.13
Neighbourhood					NS	NS
					D	E _L
					0.3146	0.0700
					429.02	364.68
					0.7417	0.4180
					40.0	177.1
					NS	36.3
					NS	14.8/1.34
					NS	NS

Note: Model ID includes specific dispersal kernel in subscript; lognormal (L), exponential (E), and lognormal-clipped (LC), exponential-clipped (EC), NC: model did not converge, NS: non-significant. The two values within the dispersal column refers to the estimates of B/β for the exponential kernel and X_0/X_b for the lognormal kernel. Abbreviations: AIC, Akaike's Information Criterion; MDD, mean dispersal distance; STR, standardized total recruits.

recruitment stage, where model fit was better for the 2015 assessment year (stage 1:0.451 and stage 2:0.321) than those which occurred in the 2016 assessment year (stage 1:0.156 and stage 2:0.093). Species-specific recruitment models performed best overall for ACSA ($R^2 = .352$) and worst for ABBA ($R^2 = .211$) among tree species which were present across all three sites. For species present within only one or two sites, POTR at Le Bic ($R^2 = .412$) had the best fit overall across recruitment stages and years, while BEPA at Abitibi had the poorest model overall ($R^2 = .099$, Table 2).

3.3 | Substrate favourability

We found that the favourability of certain substrates directly influences the distribution of seedling densities, and thus supported our second prediction. Overall, 21 of the final 56 recruitment models included substrate favourability (Table 2), where the relative influence differed amongst sites, recruitment stages, species and years (Table 3). However, we found only a few consistencies with the favourability of substrates. First, temperate tree seedling densities were significantly and negatively impacted by the presence of boreal-associated substrates: needle cover (ACRU: $f = 0.108$, ACSA: $f = 0.013$, BEAL: $f = 0.038$ and FAGR: $f = 0.043$) and decayed wood (ACRU: $f = 0.145$, ACSA: $f = 0.130$ and FAGR: $f = <0.001$). Interestingly, ABBA was favoured by these two conspecific substrates (needle $f = 0.310$ and decayed wood $f = 0.657$), at least at the Abitibi site. Second, we found that temperate canopy-associated substrate, leaf cover, was found to be extremely unfavourable for boreal species ($f = 0.184$) and certain temperate species (ACRU: $f = 0.212$ and ACSA: $f = 0.167$), but not others (BEAL: $f = 0.486$ and FAGR: $f = 0.358$; Table 3). Finally, regardless of species, we found that the single best predictor of tree seedling densities was the presence of deciduous plant cover within the recruitment plots (global average across all species, $f = 0.589$). Deciduous plant cover overall was highly favourable across species at both Abitibi (site avg. $f = 0.885$) and Le Bic (site avg. $f = 0.781$), but unfavourable at Sutton (site avg. $f = 0.225$). Deciduous plant cover was also found to be more favourable across all species for stage 2 recruitment than stage 1, particularly at Le Bic (1: $f = 0.696$ and 2: $f = 0.848$) and Sutton (1: $f = 0.081$ and 2: $f = 0.369$; Table 3).

Substrate favourability was consistent across years for most species and recruitment stages. However, certain exceptions did exist. For example, deciduous plant cover was unfavourable for both recruitment stages of ACSA at Le Bic in 2015 ($f < 0.250$), but then became favourable in 2016 ($f = 0.999$). The opposite can also occur, where deciduous plant cover was favourable at Sutton in 2015 ($f = 0.981$) for stage 2 ACSA but not the following year in 2016 ($f < 0.001$; Table 3).

3.4 | Seedling dispersal

Dispersal was found to be a key driver of tree seedling recruitment as it was included within 31 of the final 56 models (Table 2). We found that mean distance dispersal (MDD) for the most parsimonious models, regardless of the clipped or non-clipped dispersal analyses, was within 20.0 m when averaged across all factor

TABLE 3 Summary of substrate favourability for the most parsimonious models by species, seedling stage, year and site

Substrate favourability	Abitibi						Le Bic						Sutton					
	Stage 1			Stage 2			Stage 1			Stage 2			Stage 1			Stage 2		
	2015	2016	2015	2015	2016	2015	2015	2016	2015	2016	2015	2016	2015	2016	2015	2016	2015	2016
ABBA																		
Moss	0.361 (0.009–1.0)	NS	<0.001 (0.0–0.267)	NS	NS	NS	<0.001 (0.0–0.042)	0.230 (0.083–0.477)	NC	NS	NS	NS	NS	NS	NS	NS	NS	NS
Needles	0.406 (0.025–0.994)		0.215 (0.025–0.548)				0.013 (0.002–0.021)	<0.001 (0.0–0.050)										
Leaves	0.148 (0.037–0.623)		0.507 (0.080–0.919)				0.047 (0.043–0.092)	0.033 (0.014–0.079)										
Deciduous	0.976 (0.799–0.999)		0.566 (0.060–0.999)				0.993 (0.935–1.0)	0.999 (0.646–1.0)										
Decayed	0.464 (0.095–0.999)		0.850 (0.125–1.0)				0.0393 (0.002–0.144)	<0.001 (0.0–0.240)										
ACRU																		
Moss	NS	NC	<0.001 (0.0–0.441)	NS	0.026 (0.0–0.201)	0.238 (0.077–0.380)	<0.001 (0.0–0.026)	NS	Species Absent									
Needles			0.242 (0.006–0.677)		0.077 (0.013–0.156)	0.112 (0.033–0.188)	<0.001 (0.0–0.015)											
Leaves			0.563 (0.150–0.991)		0.016 (0.0–0.079)	0.235 (0.083–0.352)	0.034 (0.014–0.069)											
Deciduous			0.998 (0.189–0.999)		0.809 (0.141–1.0)	0.976 (0.354–1.0)	0.999 (0.479–1.0)											
Decayed			0.348 (0.003–0.992)		0.232 (0.024–0.722)	<0.001 (0.014–0.243)	<0.001 (0.0–0.030)											
ACSA																		
Moss	NS	NS	<0.001 (0.0–0.122)	NS	0.352 (0.012–1.0)	<0.001 (0.0–0.055)	0.0015 (0.0–0.132)	<0.001 (0.0–0.543)	0.067 (0.0–0.030)	0.999 (0.151–1.0)	0.999 (0.344–1.0)							
Needles			<0.001 (0.0–0.043)		<0.001 (0.0–0.183)	0.104 (0.005–0.234)	<0.001 (0.0–0.041)	<0.001 (0.0–0.274)	0.096 (0.0–0.256)	<0.001 (0.0–0.622)	0.002 (0.0–0.877)							
Leaves			0.277 (0.027–0.481)		0.151 (0.093–1.0)	0.180 (0.022–0.330)	0.008 (0.003–0.081)	0.113 (0.015–0.999)	0.067 (0.065–0.174)	0.235 (0.084–0.434)	0.286 (0.08–0.877)							
Deciduous			0.999 (0.100–1.0)		<0.001 (0.0–0.999)	0.999 (0.132–1.0)	0.252 (0.160–1.0)	0.998 (0.154–1.0)	0.981 (0.212–1.0)	0.981 (0.183–1.0)	<0.001 (0.0–0.245)							
Decayed			<0.001 (0.0–0.2575)		0.045 (0.0–1.0)	<0.001 (0.0–0.136)	0.015 (0.0–0.307)	<0.001 (0.0–1.0)	0.109 (0.096–0.293)	0.998 (0.060–1.0)	<0.001 (0.0–0.247)							
BEAL																		
Moss	Species Absent				Species Absent													
Needles																		
Leaves																		
Deciduous																		
Decayed																		

(Continues)

TABLE 3 (Continued)

Substrate favourability	Abitibi				Le Bic				Sutton			
	Stage 1		Stage 2		Stage 1		Stage 2		Stage 1		Stage 2	
	2015	2016	2015	2016	2015	2016	2015	2016	2015	2016	2015	2016
FAGR	Species Absent											
Moss	Species Absent											
Needles									NS	NS	<0.001 (0.0–0.124)	0.272 (0.0–0.999)
Leaves											0.043 (0.196–1.0)	<0.001 (0.0–0.999)
Deciduous											0.069 (0.014–0.087)	0.649 (0.269–1.0)
Decayed											<0.001 (0.0–0.029)	0.497 (0.054–0.999)
											<0.001 (0.0–0.044)	<0.001 (0.0–0.999)

Note: BEPA and POTR are absent as substrate favourability was not included within the final model selections for these species. 95% confidence limits of parameter estimates are (in parenthesis). NC: model did not converge. NS: non-significant.

combinations (Table 2, Figure 5). Overall, ACSA had the longest MDD by species on average (31.6 m), POTR the shortest (8.2 m), while all other species generally were around 15.0 m (Table 2). We found that the lognormal dispersal kernel provided a much better fit (29 out of 31) than the exponential kernel (Table 2). The non-clipped analysis was favoured in 20 of the final 31 models, particularly by *Acer* species (10 non-clipped: 1 clipped). Seedling dispersal of ABBA (4:5), BEPA (2:3) and FAGR (1:2) showed no preference for clipped or non-clipped dispersal (MDD was well within 20.0 m for these species). POTR favoured the more localized recruiting clipped analysis (0:3) (Table 2).

3.5 | Neighbourhood (*Pb*)

We found very little support for the influence of hetero-specific neighbourhood (<20.0 m of recruitment plot centre). The effect of the neighbourhood was significant in only 6 of the 56 total models (Table 2), where the influence of neighbourhood composition (as indicated by a high *Pb* estimate) on recruitment was weak (*Pb* < 1.11, Tables 2 and 4). We found no clear relationship with site, species, nor recruitment class or year of assessment.

4 | DISCUSSION

Our study linked fecundity, dispersal, substrate favourability and local neighbourhood as a means of explaining the recruitment of trees at the temperate-boreal ecotone of northeastern North America. We provide novel evidence that priority effects are inhibiting the recruitment of temperate species into the boreal forest. Our findings suggest that the relative strength of the priority effects imposed on temperate tree species is, however, dependent on the site, species, recruitment stage and year. The variability among our models reveals the difficulty of modelling seedling recruitment (Benavides et al., 2016; Bin et al., 2011; Caspersen & Sprunoff, 2005). Nonetheless, our extensive dataset and models allowed us to outperform (~28.0% of the total variation explained) those who ran similar recruitment studies (Bin et al., 2011).

4.1 | Substrate favourability

We found an association between the distribution of certain substrates and canopy tree composition. For example, ABBA and BEPA seedlings were associated with a higher frequency of needle, moss and/or decayed wood under boreal tree canopies (Figures 2, 3, 4). Our results confirm our hypothesis that priority effects from boreal species create substrates that ultimately impede the recruitment of temperate tree species. The primary boreal type of substrate, needle cover, was particularly efficient at inhibiting recruitment of temperate tree species, in particular for *Acer* species (*f* = 0.115). Typically, boreal forest substrates are characterized as being thick, acidic and drier when compared within other forest floors (Collin et al., 2018). The acidification of soils under conifer stands is a general phenomenon (Cole, 1985). Low soil pH leads to high concentrations of soluble

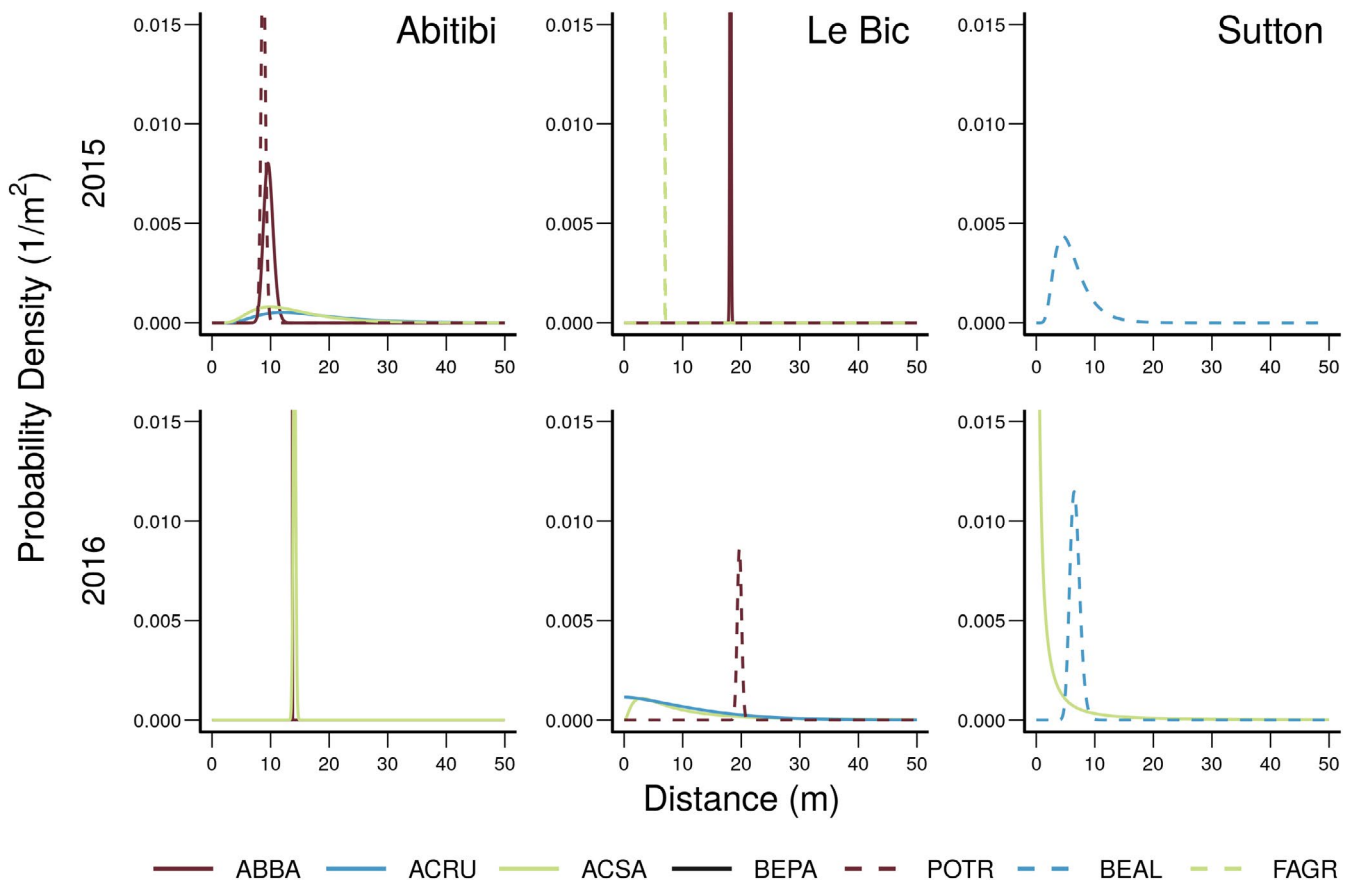


FIGURE 5 The estimated dispersal kernel for the most parsimonious model around parent trees for each of the seven tree species analysed by site and year for first-year seedlings [Colour figure can be viewed at wileyonlinelibrary.com]

aluminium that can be toxic to plants or can interfere with the uptake of calcium or other important nutrients (i.e. N, K and Mg, Kobe, Likens, & Eagar, 2002; Zak, Holmes, MacDonald, & Pregitzer, 1999). ASCA is particularly sensitive to lower nutrient availability caused by soil acidity (Collin et al., 2018; Kobe et al., 2002), which can lead to declines in health and growth at the seedling stages (Solarik et al., 2018; St.Clair, Sharpe, & Lynch, 2008). Albeit that needle cover causes significant changes to the recruitment environment for temperate tree seedlings, it was found to be more favourable ($f = 0.410$) for seedlings of ABBA. Improved boreal recruitment on heavy needle cover highlights a preference for conspecific replacement (Rooney, McCormick, Solheim, & Waller, 2000) and could further impede temperate tree species migration by limiting microsite availability. Ultimately, substrate should have a more pronounced influence on germination and first-year survival, while nutrition will impact seedling survival over the longer term.

Unlike previous studies (Caspersen & Sprunoff, 2005; LePage et al., 2000), we found that decayed wood was generally an unfavourable substrate for all temperate species, apart from one instance (ACSA_{stage2}, at Sutton in 2016). We were surprised by this finding as decayed wood has long been cited as an extremely favourable, safe site for seedling recruitment within both temperate and boreal sites (Harmon et al., 1986; Lambert, Ameztegui, Delagrangue, & Messier, 2016; Marx & Walters, 2008). Interestingly, decayed wood was a favourable substrate for smaller seeded tree species

(ABBA and BEAL) within our study, which is consistent with other studies (Caspersen & Sprunoff, 2005; Lambert et al., 2016; Marx & Walters, 2008) (Table 3). Decayed wood can provide a beneficial substrate for these species as it is easier for their smaller radical to penetrate the softer medium. Decayed wood has also been shown to contain beneficial fungi (Fukasawa, 2012), improved moisture retention and nutrient content, while improving substrate temperature resulting in improved growth (Tedersoo, Suvi, Jairus, & Kõljalg, 2008). Despite this affinity for decayed wood by ABBA and BEAL, we highlight the difficulty in making global favourability conclusions as we found variation across years, where substrate may continue to have an impact and interact with the interannual variability in climate. For example, decayed wood was found to be a strong recruitment inhibitor ($f = 0.109$) for ACSA_{stage1} at Sutton in 2015; however, a highly favourable substrate ($f = 0.998$) the following year, which was opposite of what we found for BEAL (Table 3). The low favourability of decayed wood for maples (ACRU and ACSA) may be because (a) while decayed wood may be a preferred substrate for germination, it could become less favourable for subsequent growth and survival due to potentially poorer nutrient availability over time for large-seeded species, (b) the species of decayed wood is unfavourable; Marx and Walters (2008) showed that seedling growth and density can be directly influenced by the species of decayed wood it establishes upon,

TABLE 4 Summary of descriptive statistics for each of the study sites by tree species, seedling stages (1: first-year seedlings, 2: older seedlings (≤ 30.0 cm in height), and overstorey canopy trees (DBH > 10.0 cm) for the measurement periods of 2015 and 2016

Site (mapped area)	Abitibi (4.0 Ha)				Le Bic (10.4 Ha)				Sutton (20.0 Ha)						
	Seedling Stage	2		Canopy trees	1	2		Canopy trees	1	2		Canopy trees			
		2015	2016			2015	2016			2015	2016		2015	2016	
Balsam fir (ABBA)	252 (0.63)	18 (0.045)	563 (1.41)	372 (0.93)	1,113 (5.82)	107 (0.10)	134 (0.13)	402 (0.39)	471 (0.46)	7,362 (11.19)	39 (0.02)	17 (0.009)	68 (0.034)	70 (0.035)	2,336 (3.24)
Red maple (ACRU)	164 (0.41)	1,048 (2.62)	454 (1.14)	370 (0.93)	237 (2.27)	614 (0.60)	11,389 (11.12)	225 (0.22)	221 (0.22)	2,103 (3.68)	N/A	N/A	N/A	N/A	N/A
Sugar maple (ACSA)	77 (0.19)	7 (0.018)	463 (1.16)	329 (0.82)	165 (2.68)	315 (0.31)	1920 (1.88)	612 (0.60)	241 (0.23)	495 (1.56)	1944 (0.97)	336 (0.168)	976 (0.49)	887 (0.44)	2,821 (6.61)
Paper birch (BEPa)	5 (0.01)	1 (0.003)	24 (0.06)	0 (0.0)	542 (8.02)	9 (0.001)	434 (0.424)	49 (0.05)	8 (0.007)	953 (2.04)	51 (0.02)	25 (0.013)	28 (0.014)	40 (0.02)	1,355 (3.36)
Yellow birch (BEAL)	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	235 (0.12)	326 (0.163)	183 (0.09)	249 (0.12)	3,085 (10.61)
American beech (FAGR)	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	201 (0.10)	34 (0.017)	247 (0.12)	189 (0.09)	921 (1.97)
Aspen (POTR)	N/A	N/A	N/A	N/A	N/A	11 (0.01)	0 (0.00)	60 (0.05)	13 (0.05)	1949 (5.30)	N/A	N/A	N/A	N/A	N/A
Total analysed	498	1,074	1,504	1,071	2,057	1,056	13,877	1,348	954	12,862	2,807	738	2,014	1,435	10,518

Note: Tree seedling values reported are the number individuals over the entire site, whereas values in parentheses are the average per recruitment plot, and total basal area for canopy trees (m²/Ha).

where nitrogen concentrations and mineralization rates can vary considerably between species of decayed wood and (c) climate variability; as the favourability of a given substrate may change if is impacted by reductions in precipitation or increases in temperature. Similarly, Lambert et al. (2016) showed that although conifer and birch decayed wood was found to be highly very favourable for BEAL, maple decayed wood was not.

The best single predictor of tree seedling density across species and sites within the temperate-boreal ecotone was the presence of deciduous plant cover within our recruitment plots (Table 3). All species (except BEAL) recruitment were positively associated with the presence of deciduous vegetation. These findings have been reported in other recruitment studies (Benavides et al., 2016; Ibáñez et al., 2015), where the herbaceous cover has been shown to improve tree seedling emergence and survival by offering shade and reducing transpiration demands (Muhammed, Touzard, Bagousse-Pinguet, & Michalet, 2013). Deciduous cover has also been suggested as providing protection from early spring frosting events (Morin & Chuine, 2014), and refuge from herbivory (Solarik, Lieffers, Volney, Pelletier, & Spence, 2010). These benefits could play an extremely important role for seedling recruitment, particularly in the context of populations at the range margin as seedlings within the ecotone are already exposed to higher environmental variability (Boulangeat et al., 2012), and these added benefits could improve survival within these marginal conditions (Castro, Zamora, Hódar, & Gómez, 2004). On the contrary, an increased presence of deciduous cover could also impede early seedling recruitment through the direct competition for nutrients, light and water (Davis et al., 1999), which would ultimately reduce growth and survival of seedlings and saplings (Fei & Steiner, 2008). We have some evidence for this with $ACSA_{stage1}$ ($f = 0.296$); however, favourability of deciduous cover improved greatly for older ACSA seedlings ($f = 0.646$). Although we did not directly measure light, we assume that the increased presence of deciduous plant cover within our recruitment plots was due to higher light availability caused by gaps in the canopy (Schumann, White, & Witham, 2003). Although Caspersen and Sprunoff (2005) failed to find a consistent argument for light limitation within their recruitment study, they were able to conclude that seedling densities of ABBA and ACSA declined with decreasing light availability. Similarly, Gasser, Messier, Beaudet, and Lechowicz (2010) found declining density of ACSA and BEAL seedlings with decreasing light availability. The distribution of vegetation could indicate the variability in light availability, and therefore influence the transition of first-year seedlings to older seedlings (Benavides et al., 2016; Messier, Parent, & Bergeron, 1998).

4.2 | Seedling dispersal

Increased dispersal is generally expected to evolve through natural selection at expanding range margins (Hargreaves et al., 2014), especially if the ranges are dynamic and not static (Sexton et al., 2009). Although there is evidence of long-distance dispersal events occurring in the past (Clark, 1998), like others (Caspersen & Sprunoff, 2005; Fisichelli et al., 2013; LePage et al., 2000; Ribbens et al., 1994), we

found that seedlings are establishing at distances within close proximity of overstorey trees of the same species (Table 2, Figure 5). Furthermore, species migration can be further impeded due to the high inter-annual variability in seed crop production that could significantly minimize beyond range colonization rates (Gaston, 2009; Walck et al., 2011). For example, a species like ASCA, will typically mast every 3 – 7 years (Solarik et al., 2018), which could further delay species migration. A shortened dispersal has been shown to promote the coexistence of tree species through the reduction of competitive exclusion (Hubbell et al., 1999). However, if a species remains unable to disperse at greater distances, it will risk becoming maladapted to future climatic conditions (Franks, Weber, & Aitken, 2014; Kawecki & Ebert, 2004). Species unable to disperse at rates comparable to the changing climate will risk being exposed to environmental conditions which could cause significant drop-offs in fitness, especially if the future climate exceeds a certain species-specific threshold associated with their reproduction (Morin & Chuine, 2014; Solarik et al., 2016, 2018). For example, Périé, Blois, Lambert, and Casajus (2014) suggested that ACSA would need to disperse by as much as 4.9 km/year to keep up with suitable species-specific climatic conditions. On the contrary, although increasing dispersal distances provides an opportunity for greater range expansion, it also steepens the environmental gradient. For species with high MDD, expansion is limited by the adaptive plasticity of the species to these novel conditions (Gilbert et al., 2017). As highlighted here, temperate tree species expanding further into the boreal forest will face higher occurrences of unfavourable substrates, which, in turn, will magnify the priority effects imposed by boreal forest under greater dispersal (Mohd, Murray, Plank, & Godsoe, 2016).

4.3 | Neighbourhood

We found little to no evidence that allospecific canopy trees impact seedling density (Table 2). We suspect that this is due to the influence local neighbourhood being captured within the favourability of substrates and the amount of light rather than the cumulative basal area of hetero-specific trees. However, the minimal influence of hetero-specific trees could suggest that they help minimize host-specific enemies (i.e. seed predators, herbivory, pathogens), which have been shown to negatively affect conspecific recruitment (Ibáñez et al., 2015; Moorcroft, Pacala, & Lewis, 2006). Perhaps the variability in canopy composition currently occurring in the ecotone offers a 'middle of the road' compromise between boreal and temperate tree species, where the species better adapted to future climate conditions will eventually become dominant within these environments.

5 | CONCLUSIONS

A combination of priority effects caused by a feedback of canopy trees on substrate distribution, and limited seedling dispersal, together highlight a conundrum for rapid migration of temperate tree species into the boreal forest. First, we found the presence of boreal trees in the canopy

positively influenced the distribution of needle cover and decayed wood substrates. Then, together, these substrates inhibited the recruitment of temperate tree species, while favouring conspecific replacement. Second, we found that seedling dispersal was limited to areas in very close proximity of parent trees. These results raise concerns about species ability to maintain itself under new climatic conditions by tracking their climate optimums since the climate is changing more rapidly than they can move. Vissault (2016) concluded that the temperate-boreal ecotone would eventually transition to exclusively temperate forest, with, however, very little colonization of boreal forest by temperate tree species, even after considerable time (+10,000 years). Together, the modelling results and our empirical studies would suggest that without major disturbances alternative stable states might occur, at least for a long period of time, with the distribution of temperate and boreal forest static in time despite considerable climate change. The evidence of priority effects imposed by boreal trees provides an explanation for the lack of rapid migration of temperate tree species reported by Sittaro, Paquette, Messier, and Nock (2017). Ultimately, it should be expected that in the absence of forest management strategies or large catastrophic natural disturbance (i.e. fire or insect outbreak) that strongly modify substrates (Leithead, Anand, & Silva, 2010; Leithead, Silva, & Anand, 2012; Willis, Walters, & Gottschalk, 2015), the rate of colonization/spread of temperate species into the boreal forest should be expected to lag considerably behind the rate of climate change (Aubin et al., 2016). Finally, our results also highlight the difficulties in generalizing the factors that could limit tree recruitment at the transition zone between the temperate and boreal forest since the main factors changed amongst sites, recruitment stages, species and years. Alternatively, since we did not experimentally evaluate climate change in this study, we caution that because of all the proximal ecological and edaphic constituencies at play, they may in fact stabilize ecosystems, and thus allow for a slower functional rate of change and provide an opportunity for dispersal and recruitment rates to 'catch up' to climate change.

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AUTHORS' CONTRIBUTIONS

K.A.S., C.M., Y.B. and D.G. conceived the original study and designed the original sampling methodology; K.A.S. collected the tree

seedling data; K.A.S. and K.C. analysed and interpreted the data; K.A.S. led the writing of the manuscript and all authors provided feedback and contributed critically to all drafts of the manuscript.

DATA AVAILABILITY STATEMENT

Data for this study are deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.q573n5tdx> (Solarik, Cazelles, Messier, Bergeron, & Gravel, 2019). The R-code for analysis used in this study can be found at <https://doi.org/10.5281/zenodo.3516310> (<https://github.com/KevCaz/seedlingsRecruitment>).

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