

Local adaptation of trees at the range margins impacts range shifts in the face of climate change

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Abstract

Aim: The ability of tree species to track their climatic niche at rates comparable to global warming is of concern, particularly if they are constrained by local adaptation. If a species is locally adapted at its range margin, it could be beneficial for range expansion because it ensures that the genotypes colonizing new areas are the fittest, given that environmental conditions are more similar to the current ones. In trees, local adaptation can slow range expansion when climate change happens much faster than their ability to migrate.

Location: Québec, Canada.

Time period: 2013–2015.

Major taxa studied: Trees.

Methods: We investigate experimentally a series of factors thought to constrain the seedling phase at the leading edge of the distribution of a dominant tree species, sugar maple (*Acer saccharum* Marshall.). We established a seed transplant experiment using six provenances, representing the latitudinal species range, and transplanted them to 12 sites within, at and beyond the current northern species range margin.

Results: At present, northern provenances provide the best opportunity for establishment beyond the current range, where climatic conditions are more similar than those of the warmer central or southern portions of the species range. Establishment was highest within the species range, but survival rates were comparable to those at the range margin and beyond, regardless of provenance. We also found that the local climate was the most influential factor for early seedling establishment and survival; however, a lack of suitable microsites also significantly constrained recruitment.

Main conclusions: Our study highlights the complex interaction between provenance, climate and microsite conditions that is required to ensure successful seedling recruitment. Although sugar maple is currently displaying evidence for local adaptation to facilitate range shifts, it could risk maladaptation in the future if the local climate warms beyond a threshold required to ensure seed germination and a lack of favourable microsite conditions beyond the range.

KEYWORDS

biotic interactions, climate change, demography, local adaptation, migration, provenance, range shift, regeneration temperate–boreal ecotone

1 | INTRODUCTION

Rapid shifts of species geographical ranges are expected to occur along latitudinal and elevational gradients as species track their climatic niche under global warming (Duputié, Rutschmann, Ronce, & Chuine, 2015; Zhu, Woodall, & Clark, 2012). The challenge is no longer to establish whether changes will occur, but rather to estimate the rate and magnitude of the shifts occurring (Svenning et al., 2014). Concerns arise for species that may lack the ability to migrate at rates comparable to those projected for climate by the end of this century (IPCC, 2013). If a species is locally adapted at its range margin (i.e., better suited to the local environment than other populations of the same species elsewhere within the range; Kawecki & Ebert, 2004), it could prove beneficial because it ensures that the genotypes colonizing new areas are the fittest, given that environmental conditions are most similar to the current ones (Alberto et al., 2013). However, establishment lags can result in maladaptation of populations at the range margin if the environment is changing too fast, which can slow migration rates further (Chuine, 2010). Increasingly, species range shifts lagging behind the rate of climate change are being reported (Zhu et al., 2012), where the causes of such lags have been identified as factors such as dispersal limitations (Hargreaves, Samis, & Eckert, 2014), unfavourable climate (Williams, Michaelsen, Leavitt, & Still, 2010), biotic interactions (Moran & Ormond, 2015), unfavourable microsites (Brown & Vellend, 2014), and natural disturbances (Paul, Bergeron, & Tremblay, 2014). Currently, our understanding of how these factors interact and play on species migration is lacking, particularly at the earliest life stages of plants (Brown & Vellend, 2014; Sexton, McIntyre, Angert, & Rice, 2009; Svenning et al., 2014).

Trees are particularly vulnerable to rapid climate change, where a combination of immobility, time required to reach reproductive maturity, and limited dispersal can collectively result in slow demographical changes (Aitken & Bemmels, 2016). Trees are in their present location because they were able to adapt to the past local climate and environmental conditions; however, under climate change they must be able to express enough favourable phenotypic plasticity (e.g., leaf out period, flowering, onset of dormancy, growth) to ensure persistence in the future (Alberto et al., 2013; Solarik, Gravel, Ameztegui, Bergeron, & Messier, 2016). Even though trees typically possess wide geographical ranges and can generally have high genetic diversity and gene flow, these attributes do not necessarily translate to fast demographics or adaptive capacity (Alberto et al., 2013). A locally adapted population at the range margin may possess the valuable genetic variation allowing for increased fitness and improving the success of migration into nearby environments. However, uncertainty may arise if changes in climate occur rapidly and result in unfavourable conditions that slow the ability of a species to migrate (Aitken & Bemmels, 2016; Duputié et al., 2015).

Typically, a species' fitness declines towards its range limit owing to a combination of increased unfavourable abiotic and

biotic stressors that are beyond its physiological limits (Sexton et al., 2009). However, if a population can become locally adapted, it could minimize any potential mismatches in fitness and increase the likelihood of adaptation, and thus can lead to successful range shift (Anderson, 2016). For many temperate tree species, their southern range boundaries are constrained by warmer temperatures and lack of precipitation, whereas northern range boundaries are constrained by colder temperatures or natural disturbances (Alberto et al., 2013; Chuine, 2010; Paul et al., 2014). Currently, most studies with a focus on identifying the driving abiotic and biotic factors controlling seedling recruitment often ignore key bottlenecks (i.e., seed germination and early establishment phases) and rarely consider them across a species' range margin and beyond (Brown & Vellend, 2014).

We hypothesize that the demography at range limits will be constrained by local adaptation within the distribution. Here, we investigate the local adaptation of sugar maple (*Acer saccharum*) at and beyond its current northern species range limit. Sugar maple provides an ideal candidate to investigate local adaptation in its establishment phase, because it maintains a wide geographical range throughout much of northeastern North America (Godman, Yawney, Tubbs, 1990) and has been shown to express high genetic diversity (Gunter, Tuskan, Gunderson, & Norby, 2000). Although sugar maple has been projected to migrate under climate change (Boisvert-Marsh, Périé, & de Blois, 2014; Zhu et al., 2012), climate constrains its germination and establishment stages because its seeds require a prolonged stratification period to break dormancy (Solarik et al., 2016). Furthermore, the northern migration of sugar maple might also be impeded by an increase in unfavourable climate that influences the phenology of reproduction (i.e., seed development, maturation and quality; Morin & Chuine, 2014).

We established a seed transplant experiment to investigate the potential influence of local adaptation on early establishment and survival of sugar maple seedlings. Our study addresses the following central questions. Which is more influential for early establishment of sugar maple: climate or microsite? Furthermore, which provenances are best adapted to warmer temperatures and boreal microsites? We thus make the following predictions. Germination and survival of northern provenances will be: (a) highest at the current northern range limit, whereas the opposite will be observed for southern provenances; and (b) highest at microsites occurring beyond the current range (corresponding to cold and acidic soil conditions with a thick needle cover), whereas the opposite will be observed for southern provenances. We set up a fully randomized factorial design where we crossed climatic conditions, biotic environment and provenance. We did this by collecting seeds from six provenances representing the entire species range and seeded them to four sites located within the species limit, four sites at the northern range limit and four sites beyond the current species northern range limit. This experimental design allowed us to investigate local adaptation of early seedling stages, while also making inferences regarding the potential barriers for seedling establishment in new environments.

2 | METHODS

2.1 | Study area and experimental design

The study was carried out along the northern range limit of sugar maple in Québec, Canada (Figure 1). We selected sites from three bioclimatic zones: (a) temperate zone dominated by hardwoods (within the range limit), (b) mixedwood/transition zone (at the northern range limit), and (c) boreal zone (beyond the northern range limit). The temperate zone included sites that lay within the hardwood forest subzone consisting of the sugar maple–bitternut hickory (*Acer saccharum*–*Carya cordiformis*), sugar maple–basswood (*Acer saccharum*–*Tilia americana*) and sugar maple–yellow birch (*Acer saccharum*–*Betula alleghaniensis*) bioclimatic domains. The mixedwood/transition zone consisted of sites within the balsam fir–yellow birch (*Abies balsamea*–*Betula alleghaniensis*) bioclimatic domain, and sites within the boreal zone were part of the balsam fir–white birch domain (*Abies balsamea*–*Betula papyifera*) (Saucier, Grondin, Robitaille, & Bergeron, 2003). Four sites within each of the above-mentioned zones were selected from the permanent plot network RESEF (Le Réseau d'Étude et de Surveillance des Écosystèmes

Forestiers Québécois or The Québec Forest Ecosystems Research and Monitoring Network; Périé & Ouimet, 2003), which allowed us to choose sites based on comparable (between sites) upper mineral soil (0–15 cm) exchangeable calcium concentrations; a well-known limiting factor to sugar maple regeneration and survival (Moore, Duchesne, & Ouimet, 2008). All sites were undisturbed uneven-aged stands, ranging in elevation from 200 to 800 m a.s.l. Transplant sites ranged in mean annual temperature from 0.8 to 6.0 °C, and cumulative precipitation ranged from 870 to 1,292 mm annually (Wang, Hamann, Spittlehouse, & Carroll, 2016).

Seeds were collected in the late autumn of 2013 from six provenances throughout the sugar maple range (ca. 2,160 km), following a latitudinal gradient from south to north (Figure 1). Provenances were selected to encompass a wide range of climatic variability, ranging from 3.5 to 13.6 °C in mean annual temperature and between 974 and 1,268 mm in precipitation annually (Table 1). After collection, seeds were air dried until the samaras (fruiting body) became brittle, and then were placed in a mechanical tumbler to remove the wing portion from the seed. Seeds were then passed through a feed sorter, where filled seeds were separated from unfilled seeds. To ensure that we were transplanting viable seeds, we tested a subsample

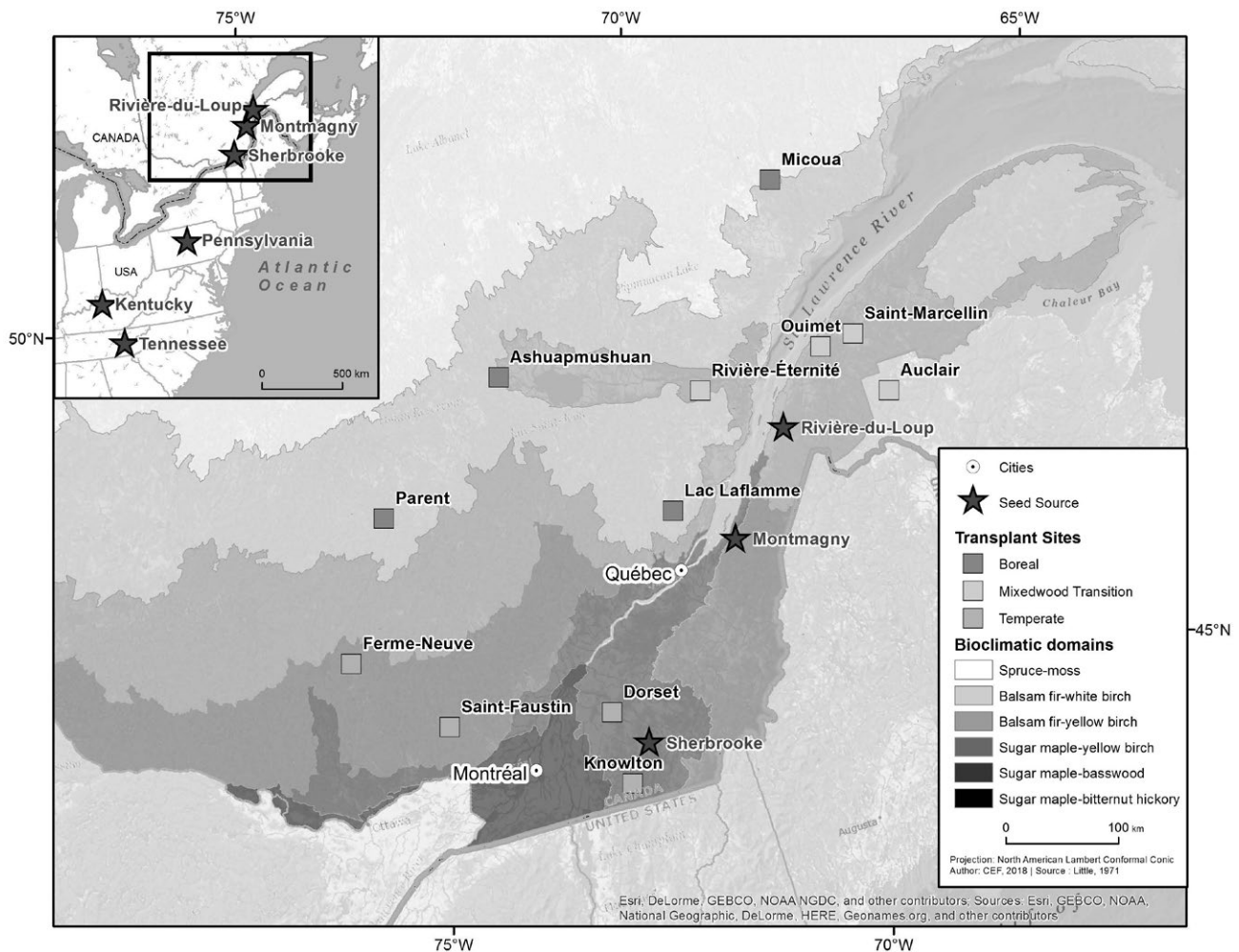


FIGURE 1 Location of transplant sites used in the study, overlaid by bioclimatic zones. Provenances used in the study are shown in figure inset

TABLE 1 Location (in decimal degrees) and climate data of the seed provenances and transplant sites used in the study

Location	Latitude	Longitude	Elevation (m)	Mean annual temperature (MAT) (°C)	Mean annual precipitation (mm)			Frost-free period (days/year)						
					Total (MAP)	Summer (May–Sept, MSP)	Snow (PAS)	Beginning (bFFP)	Period (FFP)	Total (NFFD)				
Provenances														
Tennessee, USA	35.78	-83.67	365	13.6	1,031	555	9	111	180	227				
Kentucky, USA	38.26	-84.95	262	13.2	1,123	520	17	111	183	225				
Pennsylvania, USA	41.13	-77.62	426	8.7	1,068	502	94	132	144	178				
Sherbrooke, Canada	45.49	-72.17	301	5.4	974	544	286	140	129	158				
Montmagny, Canada	46.95	-70.46	327	3.8	1,268	507	349	146	119	147				
Rivière-du-Loup, Canada	47.73	-69.48	147	3.5	1,156	456	331	147	118	145				
Transplant Sites														
Zone	Location													
Boreal	Lac LaFlamme	47.32	790	1.2	1,292	621	551	153	106	132				
	Parent	47.90	455	1.5	1,037	530	394	152	107	132				
	Micoua	49.75	190	0.8	969	458	416	160	97	123				
	Ashuapmushuan	48.81	280	2.1	870	451	302	148	115	142				
Mixedwood/ Transition	Saint Marcellin	48.30	320	2.2	1,044	462	432	153	107	133				
	Rivière-Éternité	48.23	105	3.1	983	477	331	147	118	145				
	Ouimet	48.28	335	2.3	1,041	464	424	139	111	135				
	Auclair	47.75	265	2.8	1,038	481	383	151	110	139				
Temperate	Dorset	45.82	530	5.1	1,096	532	270	144	124	161				
	Knowlton	45.19	330	6.0	1,166	564	259	138	133	162				
	Ferme Neuve	46.77	310	3.5	1,001	485	325	144	122	151				
	Saint-Faustin	46.05	415	3.9	1,097	490	376	141	126	155				

Note: Climate data (1981–2013) were generated using the Climate NA v.5.21 software package (Wang et al., 2016).

of seeds from each provenance using X-rays to ensure that viability was > 95% before transplantation at each field site. Seed lots (150 seeds/plot) were then weighed using an analytical balance in the laboratory to identify any potential differences in maternal effect caused by provenance.

At each site, 18 1-m² plots (six provenances × three replicates) were randomly established in the late autumn of 2013 (Table 1; Figure 1). Seeding began in the late autumn (ca. 1 month after natural seed dispersal), which provided two key benefits: (a) it ensured no possibility of natural seeding from the overstorey canopy falling into the plot after it was established (seeds already in plots before plot installation were removed through manual scarification); and (b) seeds were exposed to the local overwintering and early spring stratification conditions (i.e., cool, moist conditions) unique to each site. All transplant plots were positioned at a distance of ≥ 2 m from any nearby overstorey trees to minimize the influence of the bole and shading. Seed lots were then hand broadcasted evenly across each 1-m² plot. Snow was removed when already present at the time of seeding and redistributed over the seeds. We installed 1-m² metal cages (15 cm in height) over the plots to minimize the presence and impact of seed predation by granivores (i.e., squirrels, voles, and mice) and browsing by deer (see photograph in Supporting Information). We also installed *in situ* HOBO Pendant® data loggers to monitor ground-level temperature and light conditions (from December to June), providing an accurate interpretation of the below-canopy/seedling environment (De Frenne et al., 2013). In total, 32,400 seeds were distributed over 216 transplant plots at 12 sites.

2.2 | Data collection

We counted the number of first year seedlings within each of the plots in late spring–early summer of 2014. At this time, a microsite-level assessment was also conducted at the plot level, where substrate coverage (as a percentage) of each of the following variables was measured: (a) moss cover, (b) leaf litter, (c) conifer needles, (d) rock, (e) decayed logs (decay classes: 4–7; Mills & Macdonald, 2004), (f) solid wood (decay classes: 1–3; Mills & Macdonald, 2004) and (g) exposed mineral soil. In addition, an organic soil sample from the centre of each of the plots was collected to measure forest floor pH [2.00 g of soil in 20 ml of distilled water (1:10; Carter & Gregorich, 2007)]. We re-counted the presence of sown seedlings (second year) in July 2015, which were distinguished from new seedlings by the lack of cotyledons and woody tissue.

2.3 | Data analysis

An analysis of the macroscale effects of each bioclimatic zone (temperate, mixedwood/transition, and boreal) provided insight into the influence of region and canopy cover on recruitment. To do so, we analysed first and second year seedling counts each using generalized linear mixed models (GLMMs) with a negative binomial distribution and logarithmic link function because count data are often over-dispersed (Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

Additionally, we evaluated seedling survival (i.e., the proportion of first year seedlings surviving the second year) using a beta distribution with logit link function, where a constant of .0001 was added to all survival proportions to account for zeros in our data. For all GLMMs, bioclimatic zone ($n = 3$) and provenance ($n = 6$) were treated as fixed effects, whereas site ($n = 12$) was included as a random effect with a random intercept to control for unmeasured variation owing to potential spatial autocorrelation or other unmeasured effects. A backward model selection strategy was then conducted to select the best-fit model, based on the lowest Akaike's information criterion (AIC), where models within two AIC units of the minimum were also considered to have strong support (Burnham & Anderson, 2002). All statistical analyses were conducted using R v.3.4.4 (R Development Core Team, 2018), and GLMMs were fitted using the *glmmTMB* package. Likelihood ratio tests were used to assess the significance of the random effect, and the Wald Z test was used to assess the significance of fixed effects (Bolker et al., 2009). A Holm adjustment was used to correct for multiple testing across the three models (first year seedling and second year seedling count and seedling survival). In cases where significant effects were detected within a given model, a post hoc Tukey's HSD test was used for pairwise comparisons using the *lsmeans* package.

We also conducted a secondary analysis to evaluate the potential influence(s) of microsite conditions on seedling recruitment at the plot level within the mixedwood/transition zone. We focused on this area because of the within-site heterogeneity, where the distribution of temperate and boreal species tends to be clumped, creating pockets of boreal and temperate-like seedbeds (for other bioclimatic zones, see Supporting Information Figures S1 and S2). To do so, we used multiple regression tree (MRT) analysis in order to deal with nonlinear relationships and categorical data (De'ath, 2002). In short, MRT analysis produces dichotomies in a categorized manner, where the independent variables that are more similar are clustered together, whereas those that are different are split apart. It allows variance to be partitioned among different explanatory variables and their relative importance to be evaluated. The multiple dependent variables considered in these analyses were first and second year density proportions and seedling survival, and the explanatory variables included were plot-level substrate coverage (as a percentage; moss, leaf, needle, rock, decayed wood, solid wood and exposed soil) and soil pH. Additionally, we included the following site-level climate variables: (a) mean temperature; (b) number of stratification days (days in early spring, from March to May, chosen as the first month with the first positive daily temperature closest to freezing point, followed by the subsequent 2 months) with a mean daily temperature between −1 and 7 °C (determined to be the crucial temperature range required to break seed dormancy in sugar maple; Solarik et al., 2016); (c) number of warm days (days with a mean temperature of > 7 °C, between 1 March and 31 May), (d) shift ratio (the ratio of stratification days to warm days), and (e) number of days of recorded light, used as a proxy of date snow melt, which was determined as being the first day of recorded light on the HOBO logger until the day of plot measurement. Provenance was included in the

analysis as a series of provenance-specific climate data (1981–2013); (a) mean annual temperature (MAT), (b) mean annual precipitation (MAP), (c) summer precipitation (MSP, May to September), (d) winter precipitation (PAS, as snow), and (e) number of frost-free days (NFFD), frost-free period duration (FFP) and the day of the year on which frost-free period begins (bFFP) (Table 1). Finally, an additional MRT analysis was also conducted using provenance-specific climate data and elevation (in metres) to provide a proxy of seed performance. All provenance and site-specific climate data were derived using the ClimateNA v. 5.21 software package, based on the methodology described by Wang et al. (2016). All MRTs used a Euclidian distance measure to determine dissimilarities within each analysis. The final tree selection was made using the interactive ‘pick’ option by selecting the $1 - SE$ (standard error) rule. A total of 5,000 cross-validation runs were performed to ensure that we selected the correct regression tree. All data were analysed using the *mvpart* library v.1.6-0.

3 | RESULTS

A total count of 2,557 (7.8% of the total seed sown) seedlings established in the first year, of which 631 survived and were present at the re-measurement during the second year (1.95% of the total), resulting in a seedling survival rate of 24.7%. The backward model selection process based on comparative AIC values indicated a significant interaction between bioclimatic zone and provenance for first year seedling counts ($p < .001$; Table 2; Figure 2). Seedling counts were on average nearly three times more for first year seedlings (20.9 seedlings/plot) within their home range (temperate zone) when compared with the other zones (mixedwood: 7.1 seedlings/plot; and boreal: 7.5 seedlings/plot). Interestingly, seedling counts were comparable at the range limit and beyond for more northern provenances; however, seedling counts for the southern sources decreased in the mixedwood and then into the boreal zone (Figure 2). The latitudinal trend for increased seedling counts was maintained

TABLE 2 Akaike’s information criterion (AIC) and Δ AIC values of generalized linear mixed models for first year and second year seedling counts (NB: negative binomial distribution) and seedling survival (beta distribution, i.e., proportion of second year seedlings which survived through the first year)

Models	d.f.	First year (NB)		Second year (NB)		Survival (beta)	
		AIC	Δ AIC	AIC	Δ AIC	AIC	Δ AIC
Saturated model	20	1,370.49	0.0	770.57	5.7	-839.22	23.8
Stand + provenance	10	1,381.65	11.2	767.96	3.1	-848.59	8.2
Provenance	8	1,385.53	15.0	764.86	0.0	-849.44	7.0
Stand	5	1,393.26	22.8	775.09	10.2	-855.11	0.9
Null model	3	1,395.73	25.2	772.99	8.1	-855.85	0.0

Note. Saturated models included both fixed effects (stand composition and provenance) and their interaction. All models included transplant site as a random effect. Bold values denote the best model based on the lowest AIC. Model coefficient estimates, standard errors and z-statistics can be seen for both the selected (lowest AIC) and saturated models in the Supporting Information (Tables S1–S4).

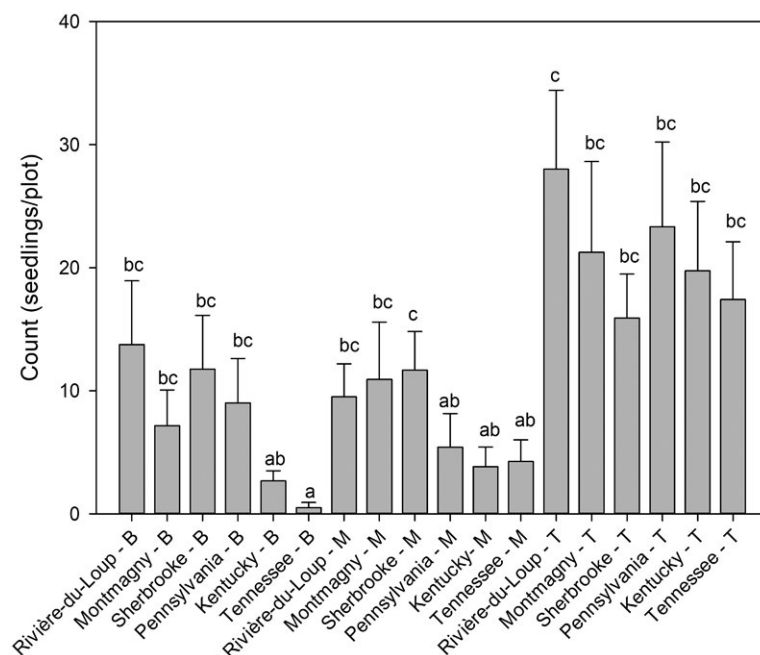


FIGURE 2 1st year seedling count (seedlings/plot) by bioclimatic zone (B: boreal, M: mixedwood/transition, and T: temperate) and provenance interaction. Bars with the same letter were not statistically different (Tukey’s HSD Test, $\alpha = .05$)

after the second year, where northern provenances had generally higher seedling counts than their southern provenance counterparts ($p < .002$; Figure 3). Survival proportions after the second year were not different by either the bioclimatic zone or the provenance.

3.1 | Microsite

The number of stratification days (recall: number of days with an average daily temperature between -1 and 7 °C) explained 57.6%

of the total variance within the six-leaf MRT of the mixedwood zone (Figure 4). Seeds exposed to < 75 stratification days ($n = 18$) had greater seedling proportions (first year: $+10.9\%$; and second year: $+2.8\%$) and higher survival rates ($+16.5\%$) when compared with sites that had a more prolonged, cooler spring (i.e., more stratification days; Table 3). Sites with more stratification days (> 75 days, $n = 54$) were further split by seed weight, where seeds weighing ≥ 0.105 g on average ($n = 15$) had higher seedling proportions (first year: $+3.6\%$; and second year: $+1.0\%$) and a higher survival ($+7.2\%$) compared with

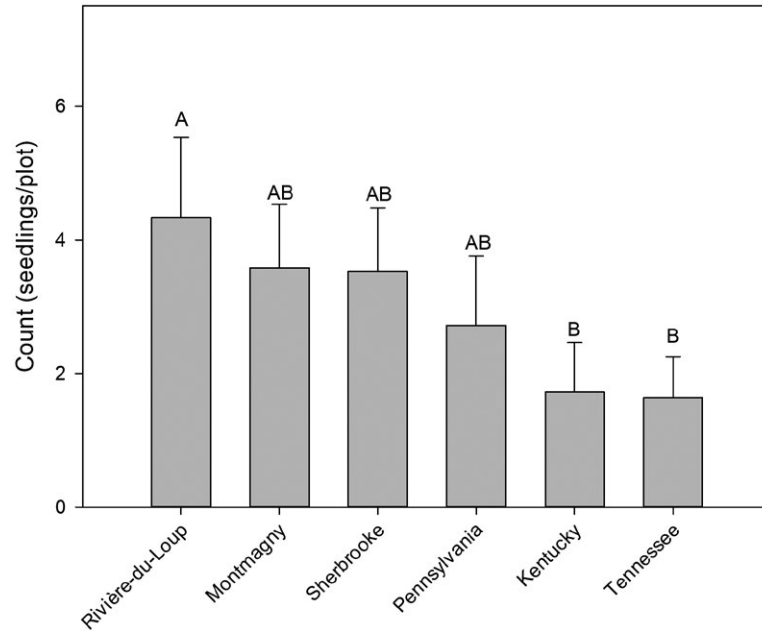


FIGURE 3 2nd year seedling count (seedlings/plot) by provenance. Bars with the same letter were not statistically different (Tukey's HSD test, $\alpha = .05$)

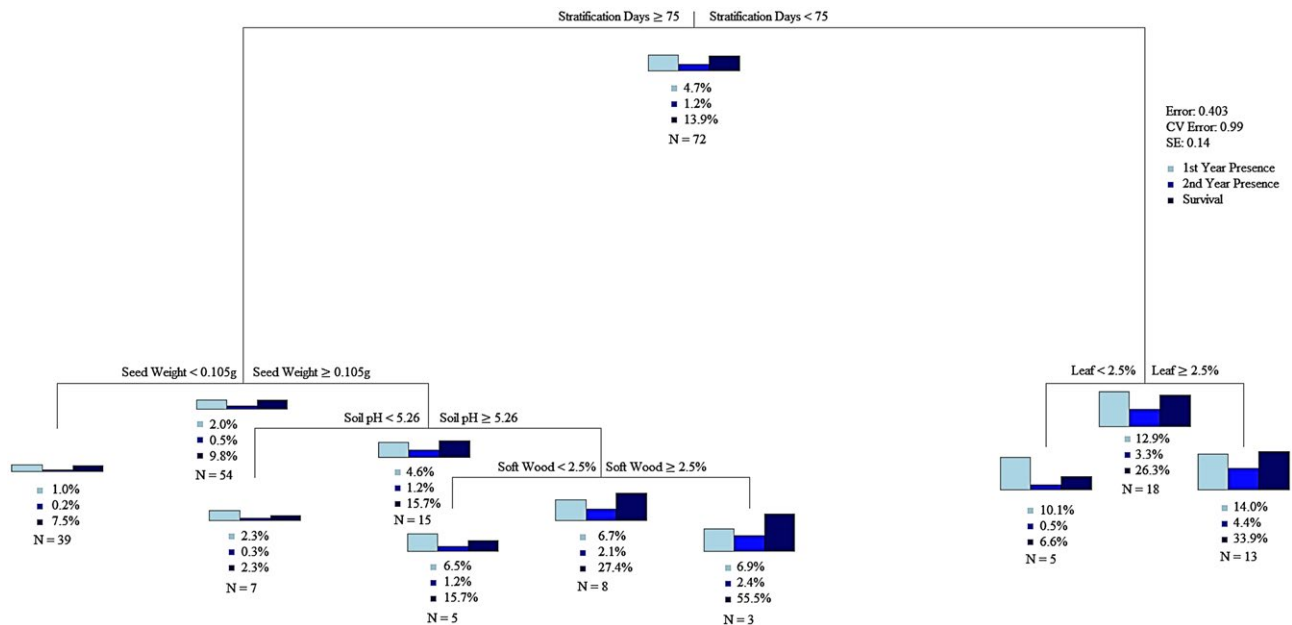


FIGURE 4 Multivariate regression tree analysis of mixedwood/transition sites for first and second year seedling presence (as a percentage) and survival (as a percentage) per 1-m^2 plot. This tree explained 59.7% of the total variance, and the vertical depth of each split is proportional to the variation explained

plots ($n = 39$) having lighter seeds (Figure 4). Higher seed mass led to greater seedling proportions within other biomes (Supporting Information Figure S2). Sugar maple established at higher proportions on more basic soils (≥ 5.26 , $n = 8$; first year: +4.4%; and second year: +1.8%), while also having nearly 10 times the survival rates (27.4 vs. 2.3%) of those seedlings establishing on more acidic ones (< 5.26 , $n = 7$). The final explanatory factor within the more basic soil plots was split by decomposed wood (i.e., soft wood), where plots covered with $\geq 2.5\%$ had nearly five times the seedling survival rates of those without (Figure 4).

A seed mass-specific MRT was best described using a three-leaf MRT, which explained 92.5% of the total variance (Figure 5). The predominant split was determined by the end of the frost-free period (78.0% of total 94.4%), where provenances experiencing a prolonged frost-free period (eFFP > 292 days) produced seeds that weighed nearly half the mass on average (.058 vs. .100 g) of those originating from provenances with an earlier end of the frost-free period (eFFP < 292 days). Summer precipitation (MSP) further explained seed mass within the earlier eFFP split, because provenances with drier summers (MSP < 549.5 mm) were found to produce heavier seeds (.104 g) than those which experienced more precipitation (.085 g; MSP > 549.5 mm). The final split occurred within the provenances with drier summer split (MSP < 595.5 mm), where seeds originating from lower elevations (< 314 m) had slightly heavier seeds (.106 g; $n = 72$) than those from higher elevations (≥ 314 m; .100 g; $n = 72$).

4 | DISCUSSION

Our study shows evidence that the local adaptation of the northern range populations of sugar maple makes them the fittest at the seedling recruitment stage. The higher seedling counts of northern provenances in its first few years is likely to help sugar maple increase its immediate response to climate warming. We found that seeds originating from provenances closer to the range margins currently provided the best opportunity to germinate and establish compared with those originating from the southern portions of the range. In addition, we showed that the strength and interplay of climate and microsite conditions together played a significant role in sugar maple recruitment. Sugar maple is highly selective of the microsite it establishes on, where the northern provenances are more likely to establish on boreal-like microsites than the southern or central provenances. Local adaptation to cold conditions does not appear to have a cost within the area we considered, because the northern provenances provided the highest seedling counts across all three climatic zones in Québec (Figure 2; Supporting Information Figures S1 and S2).

4.1 | Provenance

Results from our study highlight the importance of provenance for successful recruitment at range margins. These findings suggest

TABLE 3 Transplant site climate measurements for the initial seedling overwinter and early spring conditions (2013–2014)

Zone	Transplant site	Days measured	Mean Temperature (°C)	Stratification days (-1 to 7 °C)	Shift ratio	Negative temperature days	Days of recorded light
Boreal	Lac LaFlamme	204	-0.02	50	3.46	111	29
	Parent	211	0.88	46	2.2	100	56
	Micoua	219	1.2	40	2.87	108	46
	Ashuapmushuan	219	1.77	45	2.05	107	58
Mixedwood/ Transition	Saint Marcellin	211	2.56	95	3.38	96	42
	Rivière-Éternité	219	1.9	82	4.71	107	39
	Ouimet	211	2.08	101	4.41	106	39
	Auclair	211	2.55	68	1.96	105	58
	Dorset	204	3.15	101	2.07	63	51
Temperate	Knowlton	204	3.45	79	1.21	75	63
	Ferme Neuve	211	2.77	51	1.3	97	72
	Saint-Faustin	211	3.09	51	1.2	101	70

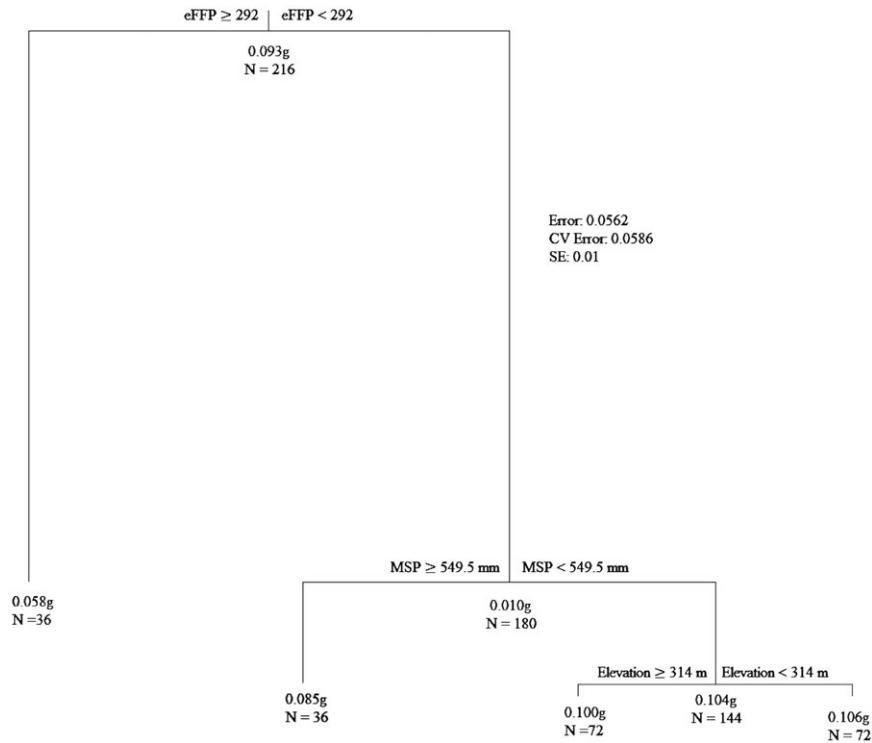


FIGURE 5 Multivariate regression tree analysis of average seed weight (in grams) determined by seed lot weight (150 seeds) used per 1-m² plot. Explanatory variables [$eFFP$ = day of the year on which the frost-free period ends; MSP = May to September precipitation (in millimetres); elevation (in metres)] consisted of provenance-specific climate data extrapolated from ClimateNA data (1981–2013). This tree explained 92.5% of the total variance, and the vertical depth of each split is proportional to the variation explained

local adaptation at these early recruitment stages and agree with our first prediction (Figures 2 and 3). Typically, parent trees living in these harsher living conditions at the range periphery would lead to a smaller, poorer quality seed crop (i.e., lower viability), which would subsequently lead to poorer recruitment rates (Walck, Hidayati, Dixon, Thompson, & Poschlod, 2011). Surprisingly, this was not the case in our study, where seeds originating in the northern range were heaviest (Supporting Information Figure S3). In addition, these populations at the margins can be exposed to more environmental variability (i.e., increased conifer species composition, colder climates) compared with their central range counterparts, which could lead to seeds that are better adapted to a wider range of conditions, including those northern conditions found beyond their current range (Anderson, 2016). Although we could not differentiate the genetic and maternal effect of provenance, performance nonetheless differed between locations of origin. First, northern provenances not only had higher seedling counts at the range margin and beyond, but they also tended to have better quality seed, indicated by a heavier mean seed mass (Supporting Information Figure S3). A heavier, larger seed provides a number of benefits from a germination perspective, which include establishing a longer radical that can penetrate the forest floor more successfully, and greater energy reserves to establish a larger seedling and allow for greater leaf formation, while also delaying the onset of carbon starvation in poorly lit understories (Walters & Reich, 2000). Lighter seeds at the southern portion of the range (which we report) have been reported previously

in other sugar maple studies (Clark, Salk, Melillo, & Mohan, 2014) and have been associated with the delay in fruit maturation caused by late flowering in these warmer environments (Morin & Chuine, 2014). The poorer recruitment rates we report from the southern provenances could also highlight the inability of these warmer conditioned (locally adapted) seeds to germinate in the cooler northern climate (Solarik et al., 2016). A meta-analysis (74 studies) performed by Hereford (2009) looked at local adaptation and fitness trade-offs and suggested that genetic drift can limit the efficacy of divergent selections of certain favourable traits. These findings suggest that the ability of a species to become locally adapted to future conditions could become reduced as the variability surrounding temperature and precipitation events in the future increases (IPCC, 2013). Our findings are reinforced by Aubin et al., (2011), who also argue that mean annual temperature increase will only have a minimal impact on trees, whereas changes in the timing of specific temperatures (i.e., time of growing season, chilling requirements, heat sum thresholds) should have a much more profound impact on demography.

4.2 | Climate

We found climate, more specifically the timing of cool and warm temperatures, to have a strong influence on sugar maple recruitment success. This effect was particularly apparent within the mixedwood and hardwood temperate zones (Figure 4; Supporting Information Figure S2). Although boreal sites did have lower overall mean

temperatures (Tables 1 and 3), mean temperature was a poor predictor of sugar maple recruitment success. Local climate has historically been found to have a significant impact on all facets of plant species phenology, life-history traits and subsequent range (Morin & Chuine, 2014), and our findings support this at the seedling establishment phase. The number of stratification days within the mixedwood/transition zone highlights the adaptation by sugar maple to the timing of temperature, where sites not meeting these specific requirements (too many stratification days can lead to significant declines in germination) experienced much lower recruitment (Figure 4). The opposite could also be true, however, where a surplus of warmer days coupled with a lack of precipitation during the summer has previously been shown to reduce recruitment in the southern range of sugar maple (Clark et al., 2014). We stress the sensitivity of germinates and seedlings to these early spring temperatures as a key driver of recruitment, which was supported across our sites.

Sites maintaining a lower shift (stratification days to warm days) ratio are more beneficial for recruitment, because they first satisfy the stratification requirements to break seed dormancy, and then a shift to warmer temperatures allows for snow melt and facilitates the establishment of seedlings (i.e., growth and photosynthesis; Table 3). On the contrary, sites with a higher shift ratio tend to occur in cooler sites, where snow remains on site longer, leading to prolonged stratification periods (Table 3; Supporting Information Figure S1). Snowpack, when present (which is the case for all of our sites), provides an ideal seed stratification environment (temperature maintained at ca. -1°C) and ultimately protects the seed/germinant from early spring frost damage (Morin & Chuine, 2014; Walck et al., 2011) and herbivory/predation. However, if snow melt is delayed (i.e., cooler spring), it can inhibit new germinates from establishing and surviving. Overall, we found an inter-site difference of 34 days in snow melt (inferred from the number of days of recorded light (Table 3). Earlier and warmer spring conditions are projected to occur under climate change (Drescher & Thomas, 2013). As a result, this would lead to earlier snow melt and accelerate spring water runoff, thus exposing seeds and seedlings to higher temperature variations that would alter and probably shorten the already sensitive stratification window. This uncertainty surrounding the timing of future climate factors (i.e., temperature, precipitation) could further reduce successful recruitment and, eventually, slow migration rates.

4.3 | Microsite

Our study showed that sugar maple was locally adapted to microsite conditions, which were evident in all the bioclimatic zones. Our findings matched our prediction that more northern provenances would tend to have higher seedling counts and greater survival beyond their range owing to this adaptation to more boreal-like microsites. More specifically, sugar maple showed a preference for substrate conditions that are most observed in hardwood temperate (a higher soil pH, increased presence of decayed wood and leaf litter) rather than boreal forests (lower soil pH, increased presence of needle cover). Although these preferences have been shown in previous

studies (Caspersen & Sprunoff, 2005), we did find that northern provenances established more readily at and beyond their current range on boreal-like microsites (needles, lower soil pH, decayed wood) than central and southern counterparts.

Increasing empirical evidence suggests that edaphic factors may even outweigh the importance of climatic factors as the primary inhibitor of tree species range migration (Brown & Vellend, 2014). It is evident that soil conditions play a crucial role in ensuring seedling establishment and survival; however, the relative influence of microsites becomes increasingly important as the likelihood of encountering more nutrient-poor soils increases northward into the boreal zone (Brown & Vellend, 2014; Graignic, Tremblay, & Bergeron, 2014). As a result, significant establishment lags could occur if temperate tree species are maladapted to establish upon boreal microsites, even if the climate becomes more favourable under climate change. Certain plant populations have been shown to adapt to specific soil types (Wright Wilcox, Stanton, & Scherson, 2006) or to the local mycorrhizal community (Kranabetter, Stoehr, & O'Neil, 2012), which appears to be the case for our southern and central provenances and less so for the northern provenances. Unlike climate, which can change rapidly, the turnover rate of soil conditions should be expected to occur over much longer time-scales and is likely to continue to play a considerable role in contributing to species migration rates in the future.

4.4 | Other constraining factors

In addition to the influence of the factors considered in the present study, a number of other important factors must be considered when discussing range shifts. The dispersal capacity of a species has long been hypothesized as being one of the primary factors to species invasion; dispersal for most wind-dispersed trees is typically highly localized and generally falls within relatively short distances ($< 20\text{ m}$) of the parent tree (Greene, Canham, Coates, & LePage, 2004). However, if seed is animal/bird dispersed or light wind dispersed (e.g., populus), it can travel much further. Ultimately, a lack of long-distance seed-dispersal events (Clark, 1998), combined with high inter-annual variability in seed crop production for tree species such as sugar maple, which typically masts every 3–7 years (Godman et al., 1990), could result in severe dispersal lags (Alexander et al., 2018; Caspersen & Sprunoff, 2005; Graignic et al., 2014). In the boreal zone, despite good local regeneration, intense crown fires may also limit dispersal of several temperate species (Paul et al., 2014). Seed predation is another contributing factor that could play a significant role in slowing species migration. Although we controlled seed predation within this study through the use of cages, biotic agents (e.g., predation, herbivory, disease) can significantly alter the spatial distribution and recruitment dynamics of seedlings. Although we did outline the importance of seed size, larger seeds will probably be exposed to increased risk of predation outside their native range, where temperate tree seeds are much more readily distinguishable than their often-smaller boreal counterparts (Hewitt, 1998), even though they will probably be much more limited

in abundance. Other factors, such as seed quality and seed characteristics (i.e., taste, nutritional value), will undoubtedly also play a role in the likelihood of the seed being consumed. Naturally, predation is highly variable among microsites, but the threat of further reductions in seed abundance could prove costly, especially when considering the inter-annual variability of seed production (Walck et al., 2011) coupled with low early establishment and survival rates.

4.5 | Future species ranges

Our results are limited to a single species, but the findings provide considerable insight into plausible bottlenecks to species migration. The contribution of maternal, climatic, and microsite effects on the local adaptation of a species will greatly influence seedling recruitment in the face of climate warming. We found that the northern seed provenances of sugar maple currently give a boost in fitness that will improve the species response to climate warming. However, if the climate warms beyond its requirements for stratification, it could potentially lead to maladaptation in the future.

It has been suggested that northward species range shifts of hundreds of kilometres by temperate tree species must occur to match their optimal climate conditions (McKenney et al., 2011). For example, Boisvert-Marsh et al. (2014) point to a rate of ca. 4.9 km/year for sugar maple under current and projected climate scenarios for 2050 in order to maintain its climatic niche. However, for this to occur in the most optimistic of scenarios, a number of recruitment bottlenecks must first be overcome. First, climate must be favourable enough for parent trees at the current range limit to be able to produce a sizeable, quality crop of seeds, which are dispersed in large quantities over long distances. Second, the new local climate where the seed falls must favour any species-specific climatic requirements needed to ensure subsequent seed germination. Assuming the first two steps are satisfied, the seedling then needs to establish on a favourable substrate, while simultaneously overcoming any biotic pressures (predation, herbivory, and competition) already present in the new environment. Finally, the newly established seedling must then display enough phenotypic plasticity to withstand the novel conditions associated with resource uptake (i.e., water, light, nutrients) until it reaches reproductive maturity. Essentially, these bottlenecks must all be overcome recurrently at considerable rates over extended periods of time to ensure the ability of a species to migrate at the range limit to maintain its future climatic niche.

Migrating species will probably need either to out-compete the current species already established or to delay migration until they senesce before detecting changes occurring at the adult/canopy stage (Hart, Oswalt, & Tuberville, 2014). Like others (Sittaro, Paquette, Messier, & Nock, 2017; Zhu et al., 2012), analysing the seedling and sapling size classes particularly within the range margins can provide insight into range expansion/contraction (Lenoir, Gégout, Pierrat, Bontemps, & Dhote, 2009; Sexton et al., 2009). Tree migration rates could also be sped up artificially with implementation of various forest management schemes, with the removal of

native northern boreal trees in favour of planting/seeding temperate tree species beyond their current limit.

These findings must be taken with caution within the context of rapid climate change. If the climate warms faster than the ability of the species to adapt, seeds from the northern range will become more maladapted than the southern/central provenances, which could potentially lead to a lag in species migration in the future (Solarik et al., 2016). In such a situation, transplanting southern provenances to the northern range limit and beyond may provide improved recruitment rates, because these seeds are currently better adapted to warmer conditions (Aitken & Bemmels, 2016; Solarik et al., 2016).

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DATA ACCESSIBILITY

Data corresponding to this manuscript are freely available and can be accessed at either <https://www.kevinsolarik.com/research/data> or from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.j0t179b>.

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BIOSKETCHES

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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