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ORIGINAL ARTICLE

Geographical variation in reproductive capacity of sugar maple (*Acer saccharum* Marshall) northern peripheral populations

Noémie Graignic*, Francine Tremblay and Yves Bergeron

Institut de Recherche sur les Forêts, Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, QC, J9X 5E4, Canada

*Correspondence: Noémie Graignic, Institut de Recherche sur les Forêts, Université du Québec en Abitibi-Témiscamingue, 445 Boul. de l'Université, Rouyn-Noranda, QC, J9X 5E4, Canada.
E-mail: noemie.graignic@uqat.ca

ABSTRACT

Aim Several models have predicted that, with climate change, Northern Hemisphere species will migrate northwards from their present distribution ranges. Sugar maple (*Acer saccharum* Marshall) reaches its northern continuous distributional limit in north-eastern North America at the transition between boreal mixed-wood and temperate deciduous forest. Our objective was to determine whether lower sugar maple recruitment potential accounts for this gradual transition between the continuous and discontinuous zones of the distribution.

Location The northern limit of sugar maple in eastern Canada.

Methods We analysed the reproductive capacity of sugar maple populations along three latitudinal transects (located in the west, centre and east of Québec) in 24 sites located between 45°51′–48°59′ N and 70°21′–79°27′ W. The study area was divided into two zones, continuous and discontinuous, based on sugar maple stand abundance. We examined stand structure, sugar maple seed abundance and germination, and sugar maple seedling density and age structure.

Results Sugar maple regeneration was uneven-aged and similar between continuous (south) and discontinuous (north) zones. For the western transect, more filled seeds and more seedlings were recorded in the continuous zone than in the discontinuous zone. Sugar maple seedling density was positively influenced by (1) basal area of mature sugar maple and saplings of all species, and (2) July mean temperature and precipitation. Four mast seed years were identified that were well synchronized across all sites; mast seeding covaried significantly with July mean temperature and July mean precipitation of the previous year.

Main conclusions Our study clearly demonstrated an effect of climatic variables and stand characteristics on sugar maple regeneration. However, these factors did not explain the transition from a continuous to a discontinuous distribution for this species. Most of our northern sites exhibited constant sugar maple recruitment over time. These results highlight the importance of including non-climatic factors in models predicting species change in abundance.

Keywords

Climate change, discontinuous populations, north-eastern North America, northern distribution limit, Québec, seedlings, sugar maple, tree regeneration.

INTRODUCTION

Several models suggest that tree populations are capable of rapid migration in the face of climatic variation (Iverson *et al.*, 2008; Morin & Thuiller, 2009). Accordingly, the reconstruction of post-glacial vegetation in North America shows several forest tree species reaching their maximum extent in the middle Holocene, followed by contractions that could have been caused by a cooling climate (McLachlan *et al.*, 2005). Given ongoing climate changes, many species are expected to expand their ranges, which could be particularly marked for populations located at the limits of their distribution ranges (Iverson *et al.*, 2004). For example, the northern limits of many tree species are modulated primarily by

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climatic factors, mainly temperature and light availability, which constrain the chances of survival at various stages of the life cycle (Woodward, 1987). A progressive decline in reproductive success results in a reduced capacity of these species to sustain themselves and to colonize new sites (Gaston, 2009). Among various natural processes, disturbances (e.g. fire, insect outbreaks and disease) play a major role in regulating species distributions at their latitudinal limits by altering population densities and limiting reproduction capacity (Ali *et al.*, 2008). Human activities, such as agriculture and forest exploitation, are superimposed upon these factors and can contribute to habitat fragmentation, thereby accentuating the isolation of populations at a landscape scale (Vranckx *et al.*, 2012).

To date, only a few studies have specifically addressed climate effects on species that are present within transition zones between forested areas. Most of these studies have focused on species that are present in northern tree-line ecosystems (i.e. the transition zone between boreal forest and the tundra) that are very sensitive to changes in climatic conditions, and which have shown recent species expansions (Lloyd & Fastie, 2003; Caccianiga & Payette, 2006). However, recent empirical observations in North America have shown that range contraction can also be observed (Zhu *et al.*, 2012).

Sugar maple (*Acer saccharum* Marshall) is a widespread and abundant tree in north-eastern North America that reaches its northern continuous distribution range at the transition between boreal mixed-wood and temperate deciduous forests (Saucier *et al.*, 2003). It is a deciduous, shade-tolerant species (Logan, 1965) that forms uneven-aged stands (Majcen *et al.*, 1984) and has major ecological and economic value in eastern North America (Godman *et al.*, 1990). Like other tree species in the Northern Hemisphere, sugar maple is predicted to migrate northwards from its current range. In the United States, models predict decreases in abundance at the southern edge of this species' range (Iverson *et al.*, 2008) and a northward expansion that will eventually lead to an increase in sugar maple abundance towards its northern limits in Canada (Goldblum & Rigg, 2005).

Climate controls species distribution in part by affecting recruitment at different phases of sexual reproduction (Walck *et al.*, 2011). Sugar maple seeds require high soil moisture levels during germination (Janerette, 1979) and a period of stratification at low temperatures, between 1 and 5 °C, to break embryo dormancy and stimulate germination (Shih *et al.*, 1985; Godman *et al.*, 1990). Germination of northern seed sources begins one week earlier at 1 °C than at 7 °C, but the cumulative proportion of germination after 90 days is 20% higher at 7 °C than at 1 °C (McCarragher *et al.*, 2011). Sugar maple seedlings and mature trees may be affected by early leaf senescence and eventually die due to frost damage (Pilon *et al.*, 1994). Sufficient understorey light is limiting during the growing season for seedlings at northern latitudes and may lead to decreased seedling growth because the time period between seedling leaf emergence and canopy closure by mature trees is shorter in northern stands (Kwit *et al.*, 2010).

In the present study, we analysed the reproductive capacity of sugar maple populations along a climatic gradient. Our objective was to determine whether or not sugar maple recruitment differs between the discontinuous and continuous zones within its northern range. We hypothesized that sugar maple had lower recruitment in the discontinuous than in the continuous part of its range, because seed production and seedling survival are reduced by low temperatures. To test this hypothesis, we examined stand structure, seed abundance and germination, seedling density and seedling age structure in populations along latitudinal transects ranging from the southern limit of the continuous sugar maple distribution in the sugar maple–yellow birch bioclimatic domain to its northern limit in the balsam fir–white birch bioclimatic domain.

MATERIALS AND METHODS

Study area

The study was located at the northern range limit of sugar maple in Québec, eastern Canada (Fig. 1). The presence of sugar maple stands along the latitudinal gradient was estimated from the analysis of large inventory databases ('points d'observations écologiques', 'placettes permanentes' and 'placettes temporaires') of the Ministère des Ressources Naturelles du Québec (MRNQ, 2013a). The gradient was divided into two zones based on the proportion of sugar maple stands in the continuous and discontinuous zone (8.5% and 2.2%, respectively).

The continuous zone lay within the sugar maple–yellow birch (*A. saccharum* and *Betula alleghaniensis* Britton) bioclimatic domain where sugar maple is abundant. The discontinuous zone was in the balsam fir–yellow birch (*Abies balsamea* (L.) Miller and *B. alleghaniensis*) bioclimatic domain, and some northern sites were located in the transition with the balsam fir–white birch (*A. balsamea* and *Betula papyrifera* Marshall) bioclimatic domain (Saucier *et al.*, 2003). Old-growth, uneven-aged sugar maple stands were selected to be as similar as possible after an analysis of the databases (the ecoforestry maps and tessellation-based forest information system (Système d'Information FORestière par Tesselle, SIFORT) obtained from MRNQ (2013a,c). The ecoforestry maps are a result of three aerial photographic campaigns and field surveys. SIFORT uses a 14-ha grid overlaid on the ecoforestry maps. In the SIFORT database, sites that had been severely disturbed by fires, insect outbreaks or wind-throw since 1965 were identified (MRNQ, 2013c). In all sites, the diameter structures of sugar maple trees formed a reverse-J shape that is typical of uneven-aged stands (see Fig. S1 in Appendix S1 of Supporting Information).

Sites were distributed along three north–south transects (eight sites per transect) and four sites per transect per zone (Fig. 1). Eleven of those sites are old-growth or rare forests that were classified as Exceptional Forest Ecosystems (EFE; MRNQ, 2013b). Data were collected at 24 sites between 45°51′ N and 48°59′ N latitude, and between 70°21′ W and

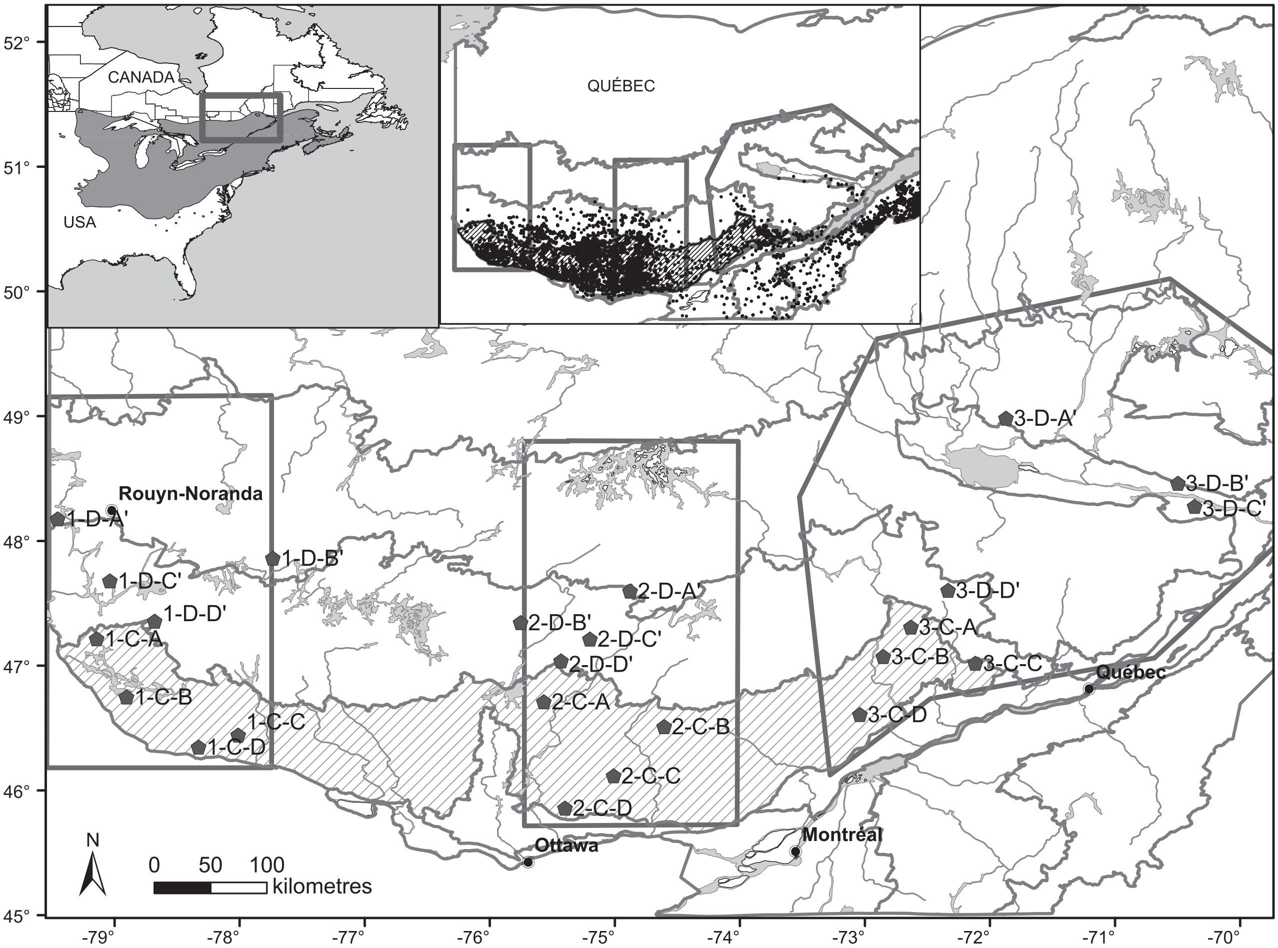

Figure 1 Map of the study area at the northern limit of sugar maple (*Acer saccharum*) distribution in Québec, showing the three transects (lines), locations of the 24 study sites (polygons; see Table S1 in Appendix S1 for more details), sugar maple–yellow birch (*Betula alleghaniensis*) bioclimatic domain (hatched), and boundary of all bioclimatic domain limits (thin line) (Saucier *et al.*, 2003). In the top middle map panel, points represents sugar maple detected in databases of the Ministère des Ressources Naturelles du Québec ('points d'observation écologiques', 'placettes permanentes' and 'placettes temporaires').

79°27′ W longitude (see Table S1 in Appendix S1), at elevations ranging between 157 and 493 m a.s.l. Climatic data for each zone and transect (1971–2010) are summarized in Table S2 (Appendix S1) and were estimated from the meteorological station nearest to each study site (Environment Canada, 2009).

Field sampling

Data were collected in 2008 and 2009. Quadrats of 0.16 ha (40 m × 40 m) were established at each site. Within each quadrat, the diameter at breast height (d.b.h. at 1.3 m) of every mature tree (d.b.h. $\geq$ 10 cm) was measured. The five largest (d.b.h.) sugar maple trees were cored in each study plot. Cores were mounted on wooden strips and sanded, and the number of rings was counted to determine their age. The ages of individuals with missing piths were estimated using correlations with trees of the same size of the missing portion of the cores. Data on age and size of trees from the same areas were available in Majcen *et al.* (1984).

The d.b.h. of every sapling (1 cm $\leq$ d.b.h. $<$ 10 cm) was measured within five circular plots (2 m radius) that were randomly distributed in the larger study plot. The age of sugar maple seedlings (d.b.h. $<$ 1 cm) was recorded in 15 circular plots of 1 m^2 that were randomly distributed across the study site. Seedlings were excavated to count all scars because sugar maple frequently develops adventitious roots along prostrate portions of stems. Age was estimated for 8822 sugar maple seedlings (total across all sites) using scars that were left each year by the loss of the scales protecting the bud of the terminal leader. Dating may be not precise for older seedlings, but this imprecision should be constant across sites. Five-year age classes were used in subsequent age structure models. When it was not possible to count the number of scars (i.e. due to stem breakage or larger basal diameter), the affected individuals were used to estimate seedling density ('undetermined' class) but were excluded from the age structure analysis.

Three seed traps, which covered a total area of 3 m^2, were randomly distributed within the 0.16-ha sample plot in two sites per zone in the western transect (transect 1 – Lac Labelle, Rémigny, Kipawa and Lac Six Milles; see Table S1). Traps were installed in July and were removed at the end of October in 2008, 2009, 2010 and 2011. Filled seeds (seeds with kernels) were checked by firmly pressing each seed between the fingers during counting. Unfilled seeds were discarded and the remaining filled seeds were cold moist-stratified at 3 °C (for a maximum of 42 days) and germinated. Germination tests were performed at the Centre de Semences Forestières de Berthier of MRNQ.

Data analysis

Data were analysed using the statistical software package R version 2.13.1 (R Development Core Team, 2011).

Forest composition

Tree species composition (presence/absence) in the 24 sites was analysed using correspondence analysis (CA, using the *cca* function in the VEGAN library; Oksanen *et al.*, 2011). Mature sugar maple trees and sugar maple saplings were excluded from this analysis because they were present in all sites.

Recruitment between zones

Variation in mature tree density and basal area was tested for every tree species (across all plots) and for sugar maple alone, using two-way analysis of variance (ANOVA) with zone, transect and their interaction as fixed effects. Density and basal area for all tree species (total) and sugar maple saplings, seed abundance and sugar maple seedling density were tested using a linear mixed-model analysis (LMM, using the *lme* function in the NLME library; Pinheiro *et al.*, 2011). For saplings, zone, transect and their interaction were treated as fixed effects in the analysis. For seed abundance, zone, year and their interaction were the fixed effects. For sugar maple seedling density responses, the fixed effects were seedling emergence year, zone, transect and their three-way interaction (seedling emergence year × zone × transect). Random effects included site for saplings and seed abundance, and site and circular plot for sugar maple seedling density. Year of seedling emergence was estimated on the basis of seedling age for the period from 1970 to 2008, plus one 'undetermined' class. The assumption of normality and homoscedasticity was verified graphically; seed abundance and seedling density data were log-transformed to respect these assumptions. ANOVA and linear mixed models were simplified by stepwise backward elimination of non-significant fixed-effect terms to produce the most parsimonious models.

Filled seeds and germination

We used generalized linear mixed-effects models (GLMM, using the *glmer* function in the LME4 library; Bates *et al.*, 2011) with a logit link function and binomial error distribution to analyse the filled seed ratio (the proportion of filled seeds to total seeds) and the germination ratio (the proportion of germinated seeds to filled seeds). In order to avoid problems in estimation, year and zone were considered to be fixed effects in two different models for each seed ratio analysis, and in one model for germination ratio; seed trap was considered a random effect. The germination ratio model was simplified by backward elimination.

Age structure

To compare sugar maple recruitment across the study area, seedlings (1–40 years old) were grouped into 5-year age classes. Sugar maple seedling age structures can be described either by a negative exponential function with constant mortality, or by a power function with a higher mortality rate in early years (Hett & Loucks, 1971). We used the Akaike information criterion (AIC; *aictab* in the AICCMODAVG library; Mazerolle, 2011), corrected for small sample sizes (AIC_c), and AIC_c weights (ω) for model evaluation (Burnham & Anderson, 2004). The power function was the best model ($\Delta AIC_c \leq 4$) for most of the 24 sites (see Table S3 in Appendix S2). It was used to estimate R (initial recruitment) and M (mortality rate) with the function $\ln(\text{stem m}^{-2} + 1) = \ln(R + 1) - M \times \ln(\text{age})$. We then used R and M to assess the effects of zones on sugar maple abundance.

The age-structure data set ($n = 24$) was not large enough to include all stand and climate variables in one model. Sugar maple seedling $\ln(R)$ was analysed using one-way, two-way or three-way ANOVA. We determined five candidate models: model 1 considered the effect of mature sugar maple basal area; model 2, mature sugar maple density; model 3, transect, zone and transect × zone; model 4 included models 1 and 3; and model 5 included models 2 and 3. We ranked each model based on AIC_c. We then computed ΔAIC_c and ω to determine the strength of evidence for each model (Burnham & Anderson, 2004). Following model fitting, we performed multimodal inference (*modavg* function in AICCMODAVG library) when required ($\Delta AIC_c \leq 4$) to assess variable effects on the initial recruitment of sugar maple. Variation in M for sugar maple seedlings was tested using two-way ANOVA with zone, transect and their interaction as fixed effects. Assumptions of normality and homoscedasticity were verified prior to analysis of $\ln(R)$ and M.

Relationships with climate

Sugar maple seedling density was compared using LMM analysis for transect × zone, or stand and/or meteorological fixed effects, with site as a random effect. Meteorological data for all sites (monthly means for 1930–2010) were obtained using the simulation software BIOSIM 9 (Régnière, 1996). We constructed different models to test the following effects: transect × zone; stand characteristics, which included total density and basal area (density and basal area included mature tree, mature sugar maple, total saplings and sugar maple saplings); climatic conditions, which included average annual temperature and precipitation, monthly average temperature and precipitation from April to October; and global models with a combination of one model of stand characteristics and one model of climate conditions. Correlations between variables were examined; total sapling density was therefore excluded from the model, because it was strongly correlated with sugar maple sapling density ($r^2 = 0.80$). Assumptions of normality and homoscedasticity were tested on all 16 global models and seedling density was log-transformed. Fits of the 27 models were compared using $\mathrm{AIC_c}$. Model averaging was performed to calculate parameter estimates and unconditional 95% confidence intervals (CI).

Mast years were compared for transect 1 using GLMM. We constructed a model based on the hypothesis that high seed production was related to warm, dry conditions in the spring of the previous year (Houle, 1999).

RESULTS

Stand characteristics

The first and second axes of the correspondence analysis (CA) accounted for 35.0% of the variation in tree species composition among sites. The first CA axis explained 22.8% of the variance (eigenvalue $\lambda_1 = 0.68$) and clearly highlighted a difference in tree stand composition between zones (Fig. 2). Towards the left-hand end of CA axis 1, most species were found only in the continuous zone (transects 1 and 2), except for mature ironwood (*Ostrya virginiana* (Mill.) K.Koch), which was also present in one site from the southern discontinuous zone (2-D-D′, Lac des Polonais). Towards the right-hand end of the first CA axis, species that were observed in the discontinuous zone are characteristic of the balsam fir–white birch bioclimatic domain (i.e. white or paper birch and trembling aspen, *Populus tremuloides* Michx.). One exception was white or American elm (*Ulmus americana* L.), which was also observed in the continuous zone. A second CA axis of variation ($\lambda_2 = 0.37$, 12.2% of the variance) distinguished sites within zones. Variation in species composition was greater within the continuous zone. For example, in continuous zone transect 2, variation was due to one species being present only once in three of the four sites sampled; this included saplings of bitternut hickory (*Carya cordiformis* (Wangenh.) K. Koch) at site 2-C-D (Lac de l'Ecluse), mature red spruce (*Picea rubens* Sarg.) at site 2-C-A (Montagne du Diable), and mature white elm at site 2-C-B (Lac Ecuyer).

Total mature tree density was higher along all transects ($F_{1,18} = 8.9691$, $P = 0.0078$) in the discontinuous zone than in the continuous zone (means of 519 stems ha^{-1} and 390 stems ha^{-1}, respectively; Fig. 3a). Total basal area was not significantly different (zones, transects or interaction zone × transect), except for total sapling basal area (Table S5 in Appendix S3).

Significantly or marginally significant differences were apparent among transects but not between zones (see Table

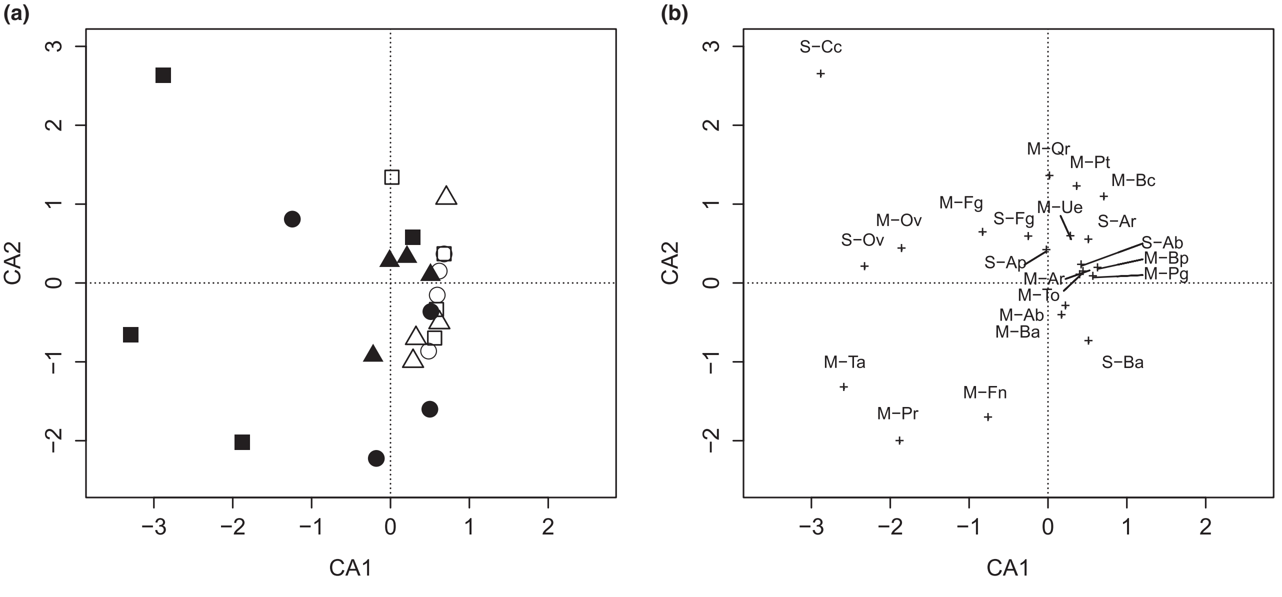

Figure 2 Ordination diagram of species presence/absence (except sugar maple, *Acer saccharum*) by site for mature trees (M; *n* = 24) and saplings (S; *n* = 24) obtained by correspondence analysis (CA) in Québec. (a) By site: Circles, transect 1; squares, transect 2; triangles, transect 3; open symbols, discontinuous zone; black symbols, continuous zone; (b) by species. CA1, correspondence analysis axis 1; CA2, correspondence analysis axis 2. Species label abbreviations: Ab, balsam fir, *Abies balsamea* (L.) Mill.; Ap, striped maple, *Acer pensylvanicum* L.; Ar, red maple, *Acer rubrum* L.; Ba, yellow birch, *Betula alleghaniensis* Britt.; Bc, mountain paper birch, *Betula cordifolia* Regel; Bp, white birch, *Betula papyrifera* Marshall; Cc, bitternut hickory, *Carya cordiformis* (Wangenh.) K. Koch; Fg, American beech, *Fagus grandifolia* Ehrh.; Fn, black ash, *Fraxinus nigra* Marshall; Qr, red oak, *Quercus rubra* L.; Ov, ironwood, *Ostrya virginiana* (Mill.) K. Koch; Pg, white spruce, *Picea glauca* (Moench) Voss; Pr, red spruce, *Picea rubens* Sarg.; Pt, trembling aspen, *Populus tremuloides* Michx.; Ta, basswood, *Tilia americana* L.; To, eastern white-cedar, *Thuja occidentalis* L.; Ua, white elm, *Ulmus americana* L.

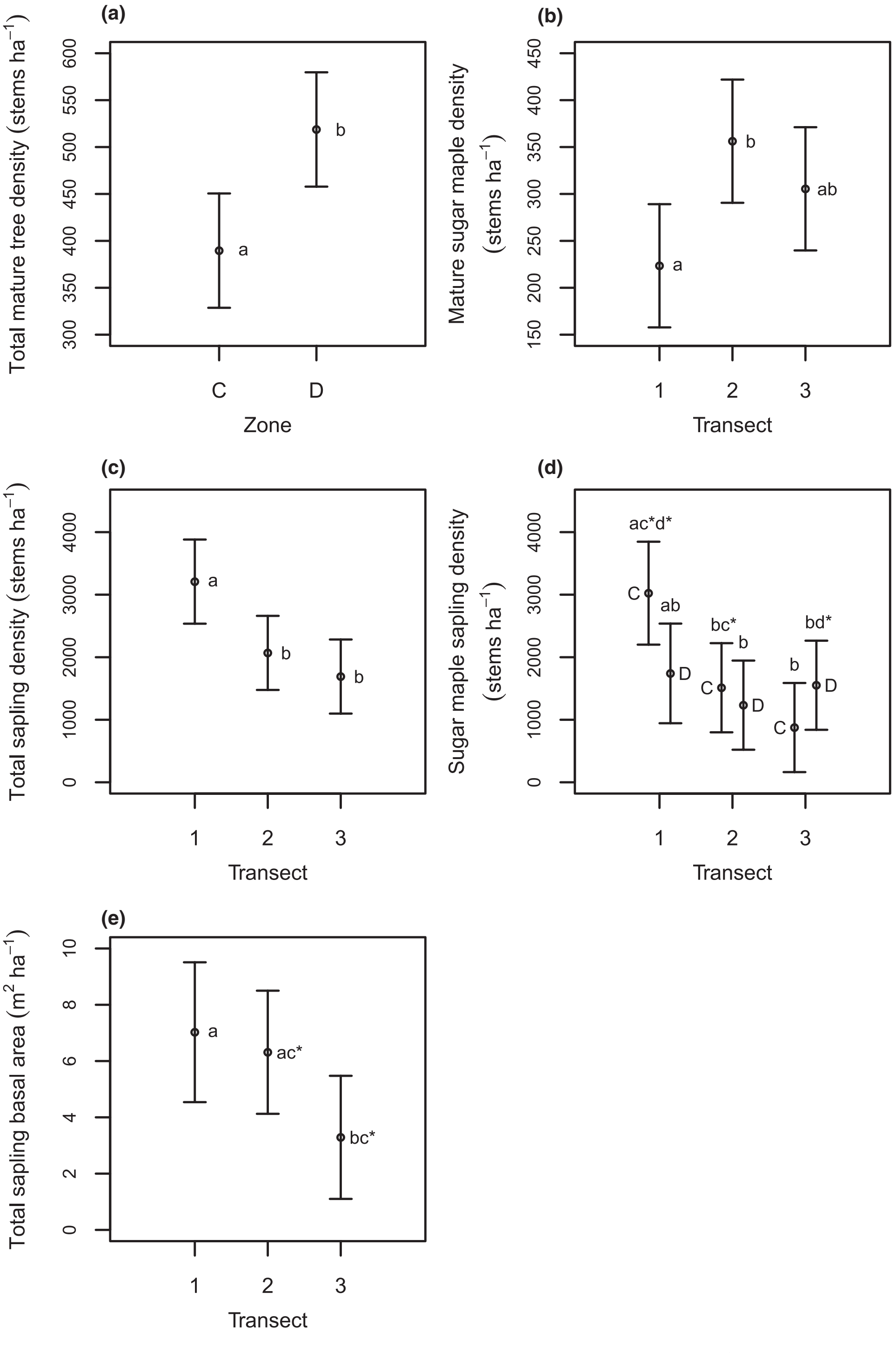

Figure 3 Predicted means (± 95% confidence intervals) of (a) total mature tree density (stems ha^{-1}; n = 24), (b) mature sugar maple (*Acer saccharum*) density (stems ha^{-1}; n = 24), (c) total sapling density (stems ha^{-1}; n = 111), (d) sugar maple sapling density (stems ha^{-1}; n = 111) and (e) total sapling basal area (m^2 ha^{-1}; n = 111) in two zones (C: continuous and D: discontinuous) or three transects (1, 2 and 3) or zones and transects in Québec. Means with the same letter do not differ at $\alpha = 0.05$ but differ (with an asterisk) at $\alpha = 0.10$.

S5) for total sapling density ($F_{2,99} = 5.8395$, $P = 0.0040$), total sapling basal area ($F_{2,99} = 2.9039$, $P = 0.0595$) and mature sugar maple density ($F_{1,18} = 3.9380$, $P = 0.0381$). Indeed, sapling densities and sapling basal area were significantly higher along transect 1 (Fig. 3c, 3209 stems ha^{-1}; Fig. 3e, 7.02 m^2 ha^{-1}) than along transect 3 (Fig. 3c, 1691 stems ha^{-1}; Fig. 3e, 3.29 m^2 ha^{-1}). Mature sugar maple density was lower in transect 1 (223 stems ha^{-1}) than in transect

2 (356 stems ha^{-1}). No differences were observed between transect 3 (305 stems ha^{-1}) and transects 1 and 2 (Fig. 3b). Sugar maple sapling densities differed among transects, but this response depended upon zone (zone × transect interaction: $F_{2,99} = 3.1813$, $P = 0.0458$; see Table S5). The highest sugar maple sapling density was encountered in transect 1 of the continuous zone (Fig. 3d, 3024 stems ha^{-1}), while no differences were found between zones within each transect.

Sugar maple seed production

Sugar maple seed production differed between years, depending upon zone (zone × year interaction: $F_{3,30} = 24.1483$, $P < 0.0001$). In 2008, seed production was higher in the continuous zone (mean 34.0 seeds m^{-2}) than in the discontinuous zone, where almost no seeds were produced (Fig. 4a). In 2009 and 2010, the seed crop was very low in both zones (mean range 0–1.8 seeds m^{-2}). In 2011, very high mean seed production was observed within the continuous zone (471 seeds m^{-2}) but did not significantly differ from that of the discontinuous zone (211 seeds m^{-2}).

The filled seed ratio varied significantly between zones and years (Fig. 4b,c). The mean ratio was higher in the continuous (0.42) than in the discontinuous zone (0.26). It was also higher in 2010 and 2011 (0.46 and 0.35, respectively) than in 2008 (0.11) or 2009 (0.00). Significant differences in germination ratios were apparent between years (2008, 0.30; 2011, 0.18) but not between zones (Fig. 4d).

Natural recruitment of sugar maple seedlings

Sugar maple seedling density varied significantly across years, zones and transects (seedling emergence year × zone × transect interaction: $F_{78,13761} = 12.23615$, $P < 0.001$). The age structure exhibited an inverse J shape, suggesting sustained seedling recruitment, especially along transect 1 (Fig. 5). In transect 1, the years 1996, 2002 and 2006 were identified as mast seed years in both the continuous and discontinuous zones (here, we assumed that higher seedling recruitment was synchronized with higher seed production during the previous year; Kelly & Sork, 2002). For each mast seed year in this transect, the continuous zone had higher seedling densities. For transect 2, 2002 and 2003 were mast years, whereas only 2003 was a mast year in transect 3. Mast seed years 1996 and 2006 were apparent in transects 2 and 3, but 1996 was not observed as a mast year in the continuous zone of transect 2.

Using a power function (Fig. 6; Fig. S2 in Appendix S3), estimated initial recruitment (R) ranged from 4.6 to 119.6 seedlings m^{-2} in the discontinuous zone, and from 2.9 to 436.0 seedlings m^{-2} in the continuous zone. As with recruitment, the range for mortality rate (M) was lower in the discontinuous zone [0.47–1.41 ln(stems m^{-2} + 1) ln(years^{-1})], but it overlapped estimates for the continuous zone [0.31–1.70 ln(stems m^{-2} + 1) ln(years^{-1})] (Fig. 6; Fig. S2). The model that tested the effects of transect and zone upon R was not the best model. Models that tested the effects of mature sugar maple basal area (model 1) or mature sugar

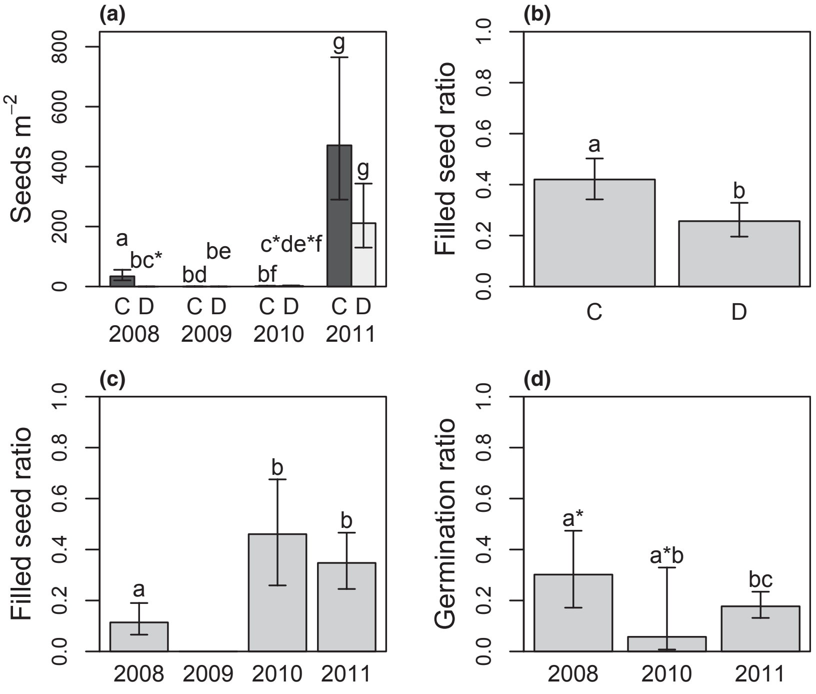

Figure 4 Predicted mean (± 95% confidence intervals) of (a) sugar maple (*Acer saccharum*) seed production (seeds m^{-2}) in C (continuous) and D (discontinuous) zones over four years (2008 to 2011; $n = 48$); (b) sugar maple filled seed ratio in two zones ($n = 5234$); (c) sugar maple filled seed ratio over 4 years ($n = 5234$); (d) sugar maple germination ratio over 3 years (2008, 2010 and 2011; $n = 1866$). Seed study was conducted only in transect 1 (Abitibi-Témiscamingue, Québec). Means with the same letter do not differ at α = 0.05 but differ (with an asterisk) at α = 0.10.

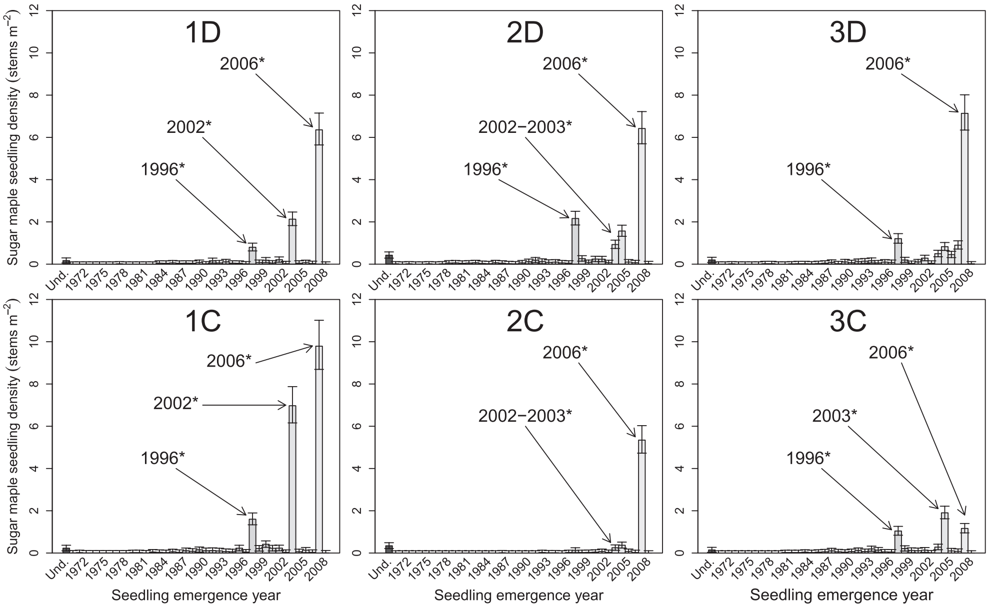

Figure 5 Predicted mean (± 95% confidence intervals) of sugar maple (*Acer saccharum*) seedling density (stems m^{-2}) for each year (Und. (undetermined) and 1970 to 2008) of C (continuous) and D (discontinuous) zones (n = 14119) in Québec. Three transects were established in each zone, e.g. 1D = discontinuous zone in transect 1. * Potential mast seed year assigned one year before seedling emergence.

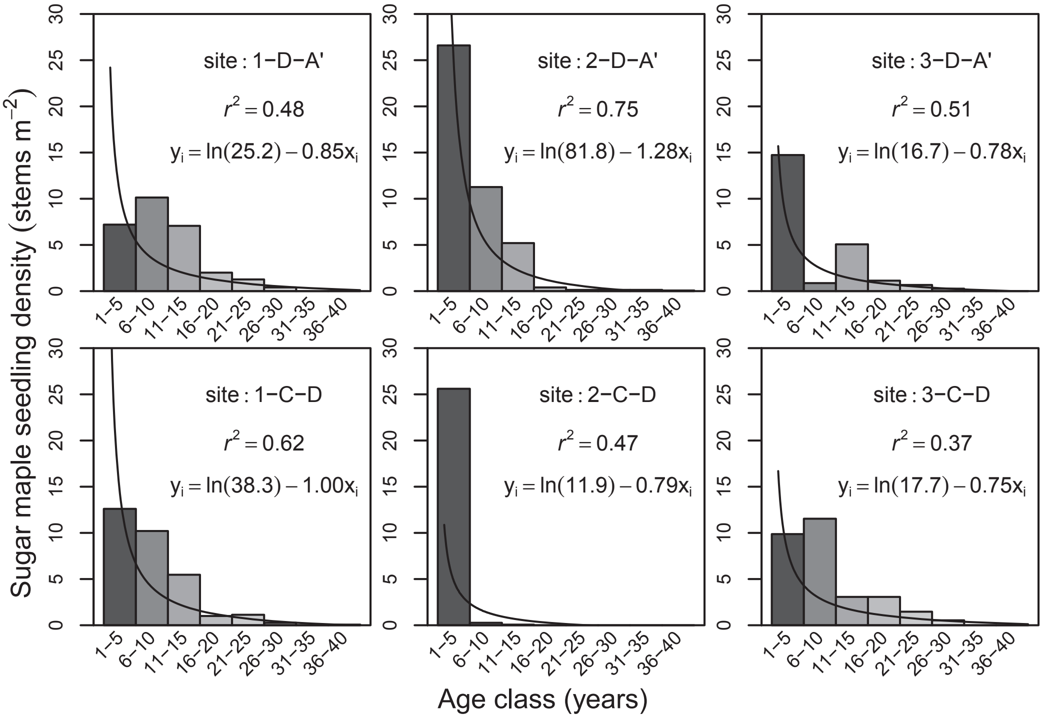

Figure 6 Sugar maple (*Acer saccharum*) age structures of the most northern and southern sites of each transect [n = 720; for all 24 sites, see Fig. S2 (n = 2880)]. For each population, the linearized form of power function is included, together with its coefficient of determination. $y_i = r - M \times x_i$; y_i is ln(stems m^{-2} + 1); r is the intercept of the curve, ln(R), where R is initial recruitment; M is the slope of the curve, mortality rate and x_i is ln(age).

maple density (model 2) on R ranked the highest among our candidate models ($\Delta\text{AIC}_c \leq 4.0$), with ω of 0.81 and 0.16, respectively. Nonetheless, multi-model inference showed no influence on R of either sugar maple basal area (model-averaged estimate: 0.043; 95% CI: −0.003, 0.089) or density (model-averaged estimate: −0.001; 95% CI: −0.006, 0.004). In brief, none of the explanatory variables that we considered could explain the variation in R. M was weakly associated

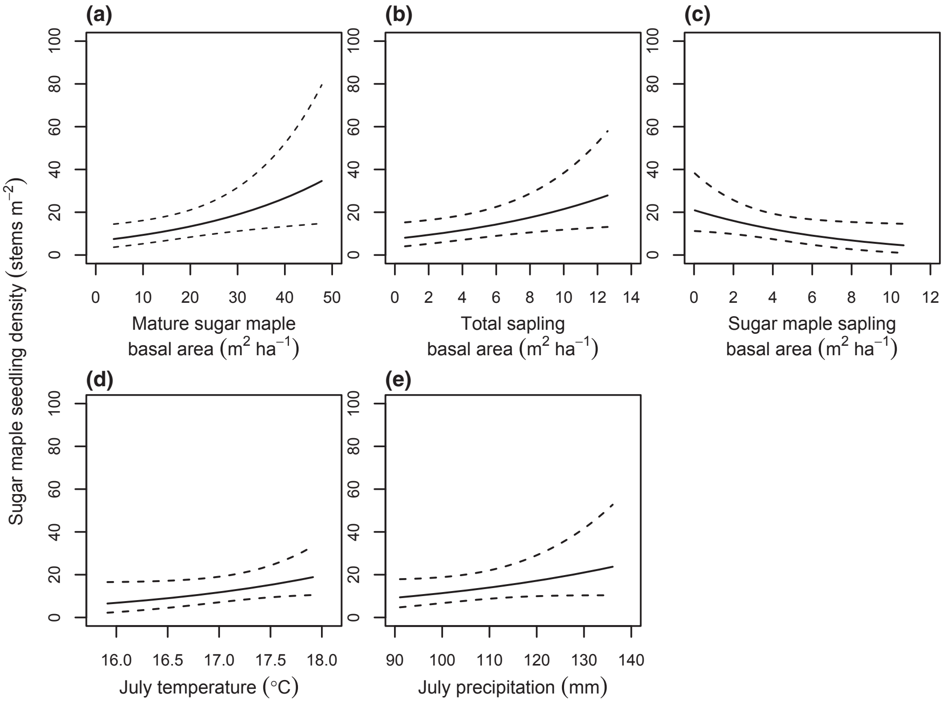

Figure 7 Predicted sugar maple (*Acer saccharum*) seedling density (stems m^{-2}) in response to all explanatory variables in the best-supported model (model 21), based on multi-model averaging of all candidate models (n = 353) in Québec. Dashed lines show 95% confidence intervals.

with geographical location (zone × transect interaction: $F_{2,18} = 3.1340$, $P = 0.0679$), with a marginally significant difference between transect 1 and 3 in the continuous zone (see Fig. S3 in Appendix S3).

Relationships with climate

Sugar maple seedling density ranged from 0.0 to 191.8 seedlings m^{-2}, with a mean of 25.5 seedlings m^{-2} in the 1-m^2 circular plots. Only 6% of the plots lacked sugar maple seedlings (4% in the discontinuous zone; 9% in the continuous zone). According to the AIC$_c$, the best model for predicting sugar maple seedling density included basal area, July mean temperature, and July mean precipitation ($\Delta\text{AIC}_c \leq 4.0$; see Table S4 in Appendix S2). The model including the zone × transect interaction ranked lowest. Parameter estimates derived from multi-model inference suggested that sugar maple seedling density increased with average July temperature and, to a lesser extent, with sapling basal area, mature sugar maple basal area and mean July precipitation (Fig. 7a,b,d,e, Table 1). Sugar maple sapling basal area had a negative effect on sugar maple seedling density (Fig. 7c, Table 1), while total mature tree basal area exerted no influence (Table 1).

Table 1 Parameter estimates and unconditional confidence intervals from multi-model inference of sugar maple (*Acer saccharum*) seedling density (ln(data + 1)) in Québec. Term abbreviations: m_BA, mature tree basal area; m_ers_BA, mature sugar maple basal area; s_BA, sapling basal area; s_ers_BA, sugar maple sapling basal area; July_T, July mean temperature; July_P, July mean precipitation.

Explanatory variables	Model-averaged estimate	95% confidence interval	
		Lower	Upper
m_BA [ln(m^2 ha^{-1} + 1)]	0.023	−0.008	0.055
m_ers_BA [ln(m^2 ha^{-1} + 1)]	0.035	0.015	0.055
s_BA [ln(m^2 ha^{-1} + 1)]	0.103	0.037	0.169
s_ers_BA [ln(m^2 ha^{-1} + 1)]	−0.139	−0.250	−0.028
July_T [ln(°C + 1)]	0.578	0.211	0.946
July_P [ln(mm + 1)]	0.023	0.004	0.041

The relationship between mast years and climatic variables was tested for transect 1. Mast seeding varied significantly with July mean temperature (Fig. 8a) and July mean precipitation (Fig. 8b) of the previous year. Predictions were valid and more than 50% probability of masting was observed when July mean temperature was > 19.5 °C and July mean precipitation was < 35 mm.

DISCUSSION

Our results indicated that sugar maple regeneration was globally similar across the discontinuous and continuous parts of its distributional range. Seedling age structures was also similar across its range with high recruitment, higher mortality at early stages, and decreasing mortality rates over time in most sampled sites. However, seedling density varied

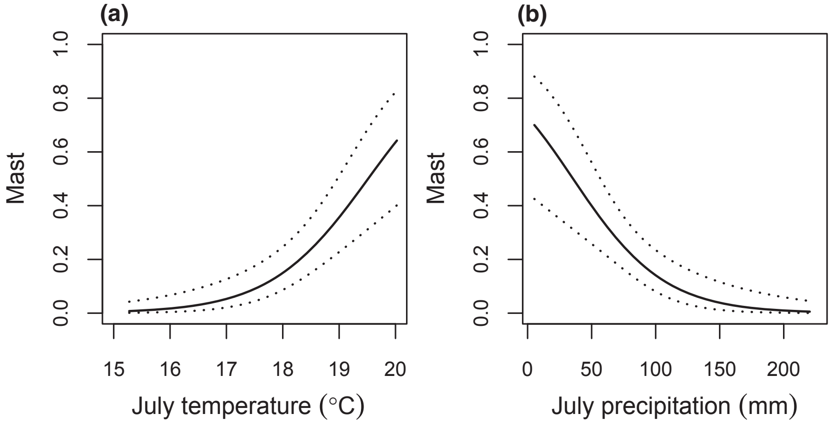

Figure 8 Predicted probability of mast seeding in sugar maple (*Acer saccharum*) for transect 1 (Abitibi-Témiscamingue, Québec; $n = 136$) based on (a) July mean temperature of the previous year and (b) July mean precipitation of the previous year. Dashed lines show 95% confidence intervals.

significantly among year (seedling emergence year), transects (west–east), and bioclimatic domains (zones). Variation in sugar maple seedling density was best explained by stand characteristics (mature tree species, mature sugar maple, tree species saplings, and sugar maple sapling basal areas) and climate conditions (July average temperature and precipitation), rather than by zonation.

Sugar maple seedling density was estimated to be 25.5 stems m^{-2}, when averaged over the 24 stands, and 32.6 stems m^{-2}, when we considered only the three northernmost sites (1-D-A′, Lac Labelle; 2-D-A′, Lac Pénobscot; 3-D-A′, Lac Patrick). These values were higher than those reported by Caspersen & Saprunoff (2005) for central Ontario (i.e. 11.1 stems m^{-2}; Haliburton Forest and Wildlife Reserve, located south of our study area), and the range of values (14.7–29.9 stems m^{-2}) that are reported by Goldblum & Rigg (2002, 2009) on the north-eastern shore of Lake Superior (Lake Superior Provincial Park; 47°45′ N, 84°42′ W). Variation in recruitment was low in our study area, in that sugar maple seedlings were absent from only 9% of circular plots in the continuous zone, which was consistent with a value of 20% for all quadrats measured by Caspersen & Saprunoff (2005). Multi-model inference indicated that five of our six first models included mature sugar maple basal area and that this variable was positively related to sugar maple seedling density (Table 1, Fig. 7, Table S4). This result was also consistent with Caspersen & Saprunoff (2005), who showed that sugar maple seedling density is correlated with higher sugar maple basal area, and with Garrett & Graber (1995), who showed that larger sugar maple trees generally producing more seeds than did smaller individuals. In contrast, Houle (1992) reported a negative relationship between sugar maple basal area versus sugar maple seed and seedling abundance, within a stand located south-east of our study area. This difference could be related to a different bioclimatic domain (sugar maple–basswood; Houle, 1992) or to stand characteristics that are not representative of a general pattern for sugar maple (Houle, 1992).

Like seedling density, basal area for mature trees (total and sugar maple) did not vary among transects and between zones. Mature sugar maple trees in transect 1 (western region, Abitibi-Témiscamingue) were larger but occurred at lower densities than those in the central region of Québec (transect 2; Fig. 3). We had expected to find larger sugar maple trees in the continuous zone where climatic conditions are more favourable to the growth of this species. Our results showed a negative influence of sugar maple sapling basal area on seedling density. The negative effect of saplings may be attributed to the shade produced by sugar maple leaves. This closed shade-cover (compared to mature trees) may induce higher sugar maple seedling mortality, even though sugar maple is a shade-tolerant species (Logan, 1965). This hypothesis of light limitation is supported by Kellman (2004), who found that sugar maple seedling mortality is lower in boreal stands than in sugar maple stands at the same latitude.

In transect 1 (west), differences between the continuous and discontinuous zones were very clear with respect to seed abundance and seedling density. In 2008, seeds were produced only in the continuous zone (34.0 seeds m^{-2}; Fig. 4). However, this trend was not observed in 2009 and 2010, where very few seeds were produced in either zone, or in 2011, where high production was observed in both zones. Only 2.5 seeds m^{-2} germinated in 2008, which was not consistent for a mast seed year, while 43.0 seeds m^{-2} germinated in 2011. On the basis of seedling density structure (Fig. 5) and seed collections, we identified four mast seed years in transect 1 (1996, 2002, 2006 and 2011). Overall, mast years were well synchronized in all sites, if we excluded 2002–2003. There was a mast year in 2002 in transect 1 (west), 2002 and 2003 in transect 2 (centre), and 2003 in transect 3 (east), which suggested a 'west–east gradient'. Four to 6 years separated each mast, which is consistent with the 3–8 years reported for Canada (Wang, 1974). Cleavitt *et al.* (2011) identified 1998, 2002 and 2006 as mast years in north-central New Hampshire. This synchronized and intermittent reproduction across the range of sugar maple could be due to endogenous rhythms (Kelly, 1994), climate conditions (Houle, 1999; Kelly & Sork, 2002), or seed predators (Tachiki & Iwasa, 2010). With respect to climate conditions, our data suggested that a warm and dry July in the previous year can induce mast seeding (Fig. 8). If some seedlings survived for several years, the presence of a seedling bank on the forest floor could compensate for the disadvantage of intermittent reproduction.

Model selection identified July mean temperature and precipitation (see Table S4) as variables positively influencing sugar maple seedling density (Fig. 7). Sugar maple seeds have high soil moisture requirements during germination (Janerette, 1979). Our results showed that precipitation during April and May did not influence seedling density. This suggested that moisture during germination was not a limiting factor. We could hypothesize that warm July temperature, combined with high precipitation, might reduce seedling mortality. However, more studies are needed to identify the direct effect of climate conditions on seedling survival in sugar maple.

Climatic models for eastern North America have predicted a mean increase of +3.3 °C (minimum, 2.1 °C; maximum, 5.4 °C) and +1% in precipitation (min. −17%, max. +13%) in June, July and August for the decade 2080–2099 compared to 1980–1999 (Christensen *et al.*, 2007). Applying these mean values with our model for the northernmost site of transect 1 (1-D-A′, Lac Labelle), our model predicted a mean increase of 5.3% (min. 2.1%, max. 18.4%) in sugar maple seedling densities for 2080–2099 compared to 1980–1999. However, the uncertainties around these estimates progressively increased as temperature and precipitation increased (Fig. 7). Therefore, our predictions are limited by these uncertainties, but an increase in sugar maple seedling density is predicted to occur with climate change.

Species distributional range-shift predictions are based on niche models, climatic envelopes, and process-based models (McKenney *et al.*, 2007; Morin & Thuiller, 2009). All of these approaches have more or less emphasized the influence of climate in predicting future species distributions, in part because other predictors are frequently unavailable. Our sugar maple seedling density model and habitat distribution models showed that the sugar maple limit was not controlled exclusively by the effect of tested climatic variables on regeneration. Therefore, northward expansion could possibly occur under different climatic scenarios (Iverson *et al.*, 2008; Morin & Thuiller, 2009). All of the sites from the discontinuous zone showed very good sugar maple regeneration. For example, the northernmost site in transect 2 (2-D-A′, Lac Pénobscot; Fig. 6) showed high sugar maple seedling densities and a typical J-shaped age structure, which indicates continuous recruitment over time. It is possible that soil characteristics (type and nutrients) could serve as explanatory factors. For example, a lack of rotten wood and leaf litter can represent a barrier to seedling establishment (Caspersen & Saprunoff, 2005), while an increase in calcium availability and a thinner litter layer are important for improving early sugar maple seedling survival (Cleavitt *et al.*, 2011). The inclusion of soil characteristics may increase the predictive power of our sugar maple seedling density model. Sugar maple regeneration could also be influenced by factors such as herbivore grazing (Salk *et al.*, 2011), seed predation (Hsia, 2009), disease (Cleavitt *et al.*, 2011), and interspecific competition (Gravel *et al.*, 2011). Accumulating evidence has shown that important non-climatic factors must be included to increase model predictive power for actual and future tree species range shifts (McMahon *et al.*, 2011).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Details of the study area: site coordinates, protection type, site and stand characteristics (Table S1), d.b.h. structure of mature sugar maple trees (Fig. S1), and climatic data for the study area (Table S2).

Appendix S2 Difference in Akaike information criterion (ΔAIC_c) and weights (ω) of age-structure models of sugar maple seedlings (Table S3), and for model comparisons of the relative importance of stand characteristics and climate conditions as predictors of sugar maple seedling density (Table S4).

Appendix S3 Results of two-way ANOVA with interaction for mature trees and linear mixed-effects models for saplings (Table S5), sugar maple age structures of all 24 sites (Fig. S2), and predicted means of sugar maple seedling mortality rate (Fig. S3).

BIOSKETCHES

Noémie Graignic is a PhD student in environmental sciences at the University of Québec in Abitibi-Témiscamingue (Canada). Her project consists of identifying factors that are influencing northward migration of sugar maple.

Francine Tremblay is a professor at the University of Québec in Abitibi-Témiscamingue (Canada). Her laboratory research interest focuses on population and conservation genetics of forest ecosystems.

Yves Bergeron is a professor of forest ecology at the University of Québec in Abitibi-Témiscamingue and University of Québec at Montréal (Canada). He is interested in forest dynamics at both the stand and landscape scales.

Author contributions: N.G., F.T. and Y.B. conceived the ideas; N.G. collected and analysed the data and led the writing of this paper.

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