


# The contrasting effects of short-term climate change on the early recruitment of tree species

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Received: 2 January 2017 / Accepted: 23 May 2017 / Published online: 1 June 2017  
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**Abstract** Predictions of plant responses to climate change are frequently based on organisms' presence in warmer locations, which are then assumed to reflect future performance in cooler areas. However, as plant life stages may be affected differently by environmental changes, there is little empirical evidence that this approach provides reliable estimates of short-term responses to global warming. Under this premise, we analyzed 8 years of early recruitment data, seed production and seedling establishment and survival, collected for two tree species at two latitudes. We quantified recruitment to a wide range of environmental conditions, temperature, soil moisture and light, and simulated recruitment under two forecasted climatic scenarios. Annual demographic transitions were affected by the particular conditions taking place during their onset, but the effects of similar environmental shifts differed among the recruitment stages; seed production was higher in warmer years, while seedling establishment and survival peaked during cold years. Within a species, these effects also varied between latitudes; increasing temperatures at the southern location will have stronger detrimental effects on recruitment than similar changes at the northern locations. Our simulations illustrate that warmer temperatures may increase seed production, but they will have a negative

effect on establishment and survival. When the three early recruitment processes were simultaneously considered, simulations showed little change in recruitment dynamics at the northern site and a slight decrease at the southern site. It is only when we considered these three stages that we were able to assess likely changes in early recruitment under the predicted conditions.

**Keywords** *Acer rubrum* · *Acer saccharum* · Climate change · Plant–climate interactions · Temperate forests

## Introduction

With the onset of global warming, the development of sound conservation and management programs for forest ecosystems will require predictions of plant population dynamics under climatic conditions that in many locations will be novel to the local plant communities (Parks and Bernier 2010). Currently, the main approach used to predict forest species responses to global warming are climate envelope models based on species' distributional ranges (e.g., Thuiller et al. 2005; McKenney et al. 2011). However, the regional outputs from climate envelope models may be spatially and temporally too coarse to generate the forecasts meaningful for management as they consider broad distributional shifts and long-term dynamics, hundreds to thousands of years (Pearson and Dawson 2003; Ibáñez et al. 2006). Given these shortcomings, multi-site demographic studies that account for the short-term responses to environmental variability among life stages and also evaluate the variability of those responses among populations can provide useful information to predict local forest dynamics under changing environments.

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Communicated by John Dwyer.

**Electronic supplementary material** The online version of this article (doi:10.1007/s00442-017-3889-1) contains supplementary material, which is available to authorized users.

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Aside from catastrophic events, adult tree survival is relatively buffered from moderate environmental change by the trees' reserves and extensive root systems (Cavender-Bares and Bazzaz 2000; Niinemets 2010; Zang et al. 2014). However, the early recruitment stages, i.e., seed production and germination and seedling establishment and survival, are highly susceptible to immediate environmental conditions (Shevtsova et al. 2009; Galvez et al. 2013); making their failure an important bottleneck in the demographic dynamic of a population (Grubb 1977; Harper 1977). Consequently, the structure of forest communities is mostly determined by the dynamics taking place during recruitment (Albrecht and McCarthy 2009; Anderson-Teixeira et al. 2013; Green et al. 2014). Thus, the most relevant information to predict short-term changes in forest structure in response to environmental change is likely linked to the recruitment process (e.g., Bykova et al. 2012; Rother et al. 2013; Kroiss and HilleRisLambers 2014).

As plants transition through different recruitment stages, i.e., seed production, seedling establishment and seedling survival, they likely require different conditions to optimize their success (Ibáñez and Schupp 2001; Perez-Ramos et al. 2013). For example, temperature may drive some processes, e.g., seed production (Horvath 2009), while water availability is the likely determinant of others, e.g., seedling establishment (De Steven 1991; Ibáñez et al. 2007). In addition, the same environmental change could have contrasting effects between life stages. For instance, increased temperature might favor seed initiation (i.e., flowering and pollination; Kumar et al. 2010), a process that for most temperate tree species usually takes place in the spring when temperatures are relatively low. However, the same change in environmental conditions might be detrimental for seedling survival late in the summer, when higher rates of evapotranspiration under warmer conditions would decrease water availability (Weltzin et al. 2001; Caldeira et al. 2014). Therefore, the effects of a varying environment on recruitment can be quite complex, and it is the combined set of dynamics that will determine the overall effect on a population recruitment success.

An additional source of variability associated with recruitment emerges from how particular populations within a species respond to the environment (Gaillard et al. 2013). Most phenological events and demographic transitions (e.g., flowering, fruiting, seedling establishment) respond to annual local environmental cues (e.g., Hoffman et al. 2010; Ziello et al. 2012; Diez et al. 2014). The year-to-year variability in the occurrence of these events has been extensively documented, and phenological dynamics have been used to make predictions about future trends under global warming (e.g., Ibáñez et al. 2010; Springate and Kover 2014; Roberts et al. 2015). However, an aspect less studied is how the same driving factor may have

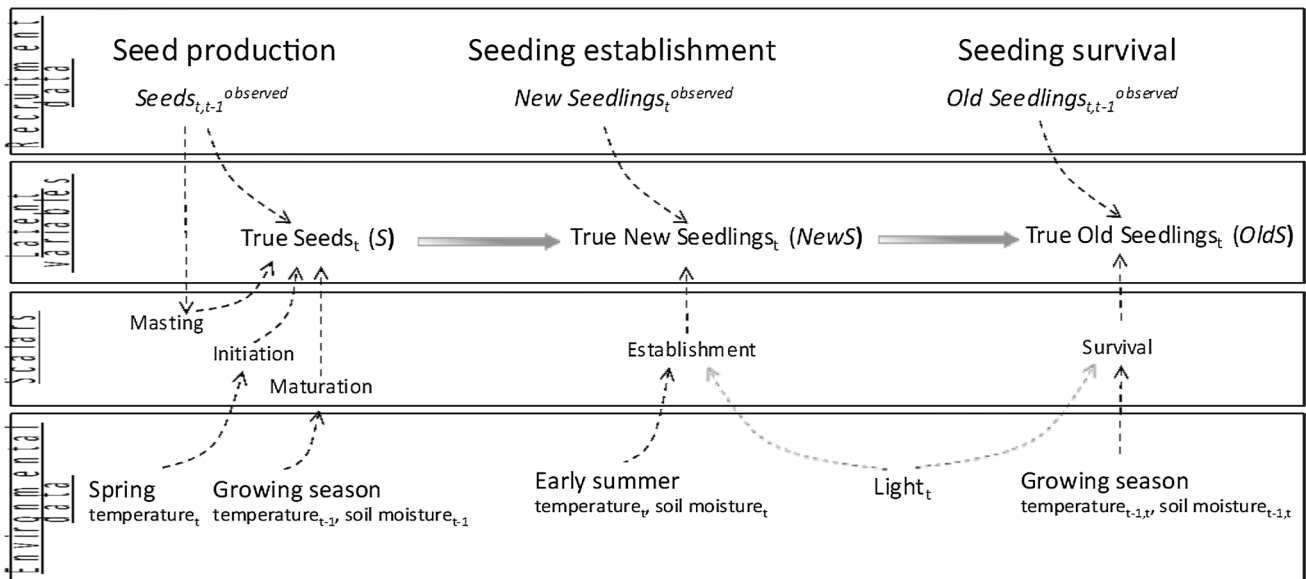
varying, or even contrasting, effects within the distributional range of the species. Populations at different climatic locations go through demographic transitions at different times of the year, e.g., flowering and seed germination can take place from early spring (lower latitude/altitude) to late spring (higher latitude/altitude) along the distributional range of a species. Thus, even if the driving factor and the magnitude of its effect are the same, populations distributed along the range of a species are likely affected by climatic clues taking place at different times of the year. This is important, because future climatic trends will not be homogenous either throughout the year or throughout the distributional range of a species (IPCC 2013). Such spatial and temporal variability would make information collected at one site unreliable for predictions in another area, i.e., climate envelope models. Still, the year-to-year variability in environmental factors and the array of responses associated with it can become an asset when we aim to predict a species response to a wide range of environmental conditions, like those forecasted under global warming (Ibáñez et al. 2013).

To generate predictions of future tree recruitment dynamics, we took into account the varying responses to environmental conditions, both between recruitment stages in a population and between populations. For 8 years, 2008–2015, we collected data pertinent to the demographic stages (seeds, new seedlings and older seedlings) that constitute the early recruitment process (seed initiation: flowering and pollination, seed maturation: fruiting, seedling establishment and seedling survival) of tree species (Fig. 1). We monitored the environmental conditions during the study period, seasonal weather and light, and analyzed the combined data sets to assess the effects of those conditions on early recruitment (Fig. 1). We also included the potential effects of masting on seed production the following year, as these may strongly affect seed output (Kelly 1994; but see Hoch et al. 2013). To assess how climate change will alter recruitment dynamics, we simulated these processes under the current climatic conditions as well as under two forecasted climatic scenarios.

## Materials and methods

### Study sites

We worked in temperate forest stands located at two latitudes in the Great Lakes region. In the northern region, University of Michigan Biological Station, Pellston, MI, 45°36'N 84°41'W, the four forests surveyed (~100 to 125 year old) represent the dominant forest types of the region: northern hardwoods, aspen, pine–aspen, and balsam fir forests. The average minimum temperature in January



**Fig. 1** Conceptual representation of the analysis showing recruitment stages (recruitment data and latent variables) and the processes affecting each transition (scalars); scalars are estimated as a function

of several variables [environmental data and seed production in the previous years (masting)]. Sub-indices,  $t$  and  $t - 1$ , indicate the years of data used in each estimation

is  $-14\text{ }^{\circ}\text{C}$ , the average maximum temperature in July is  $26\text{ }^{\circ}\text{C}$ , the annual average precipitation is 767 mm, and the growing season length (frost free period) is  $\sim 108$  days. In the southern region, University of Michigan, Ann Arbor, MI,  $42^{\circ}28'N\ 84^{\circ}00'W$ , we worked at four forest sites that host locally common forest types, oak–maple (two sites), maple–tulip poplar and oak–hickory ( $\sim 100$  to 140 year old). In this region, temperatures range from an average minimum of  $-8.3\text{ }^{\circ}\text{C}$  in January to an average maximum of  $28.8\text{ }^{\circ}\text{C}$  in July, average precipitation is 953 mm, and the length of the growing season is  $\sim 158$  days. Soils along the study sites derive from basic parent materials and have relatively high cation exchange capacity and high calcium levels (Schaeztl et al. 2012).

**Plant data**

In the summer of 2008, we placed seed traps ( $0.16\text{ m}^2$  circular meshed baskets held 1 m above the ground) and next to them delimited  $2 \times 1\text{ m}$  plots at each of our study forest sites. The seed traps and plots were set up in three rows, 20 m apart, with five seed trap–plot sample points per row, 10 m apart. We had a total of 120 sampling points (two latitudes  $\times$  four forest sites  $\times$  15 seed trap–plots). Seed traps were emptied after the two major seed release seasons, early summer (spring dispersal) and late fall (fall dispersal) each year. Seeds were sorted and identified at the species level. Plots were censused annually in early to mid-summer. New seedlings (establishing) and older seedlings ( $>1$  year old) of each species were counted. New seedlings

were identified by the presence of cotyledons and/or absence of lignified stems. We classified older seedlings as those that were  $>1$ -year-old and  $<1\text{ m}$  tall [no seedlings transitioned into the sapling stage ( $>1\text{ m}$  tall)]. Seed and seedling data were expressed in counts per  $\text{m}^2$ . One of our two studied species, *Acer rubrum* L. (Sapindaceae), grows in all sites, and the second species, *Acer saccharum* Marsh., grows in three of the four forest sites at each latitude. We chose these two species because they are not only present in most of our sites, but also because these are the species for which we have sufficient seed and seedling records to carry out the analyses (another species common at all sites was *Quercus rubra*, but the seed and establishing seedling records were very poor).

*Acer rubrum* is a mid-canopy species widely spread in eastern North American forests. Flowering, wind pollination, fruiting and seed dispersal by wind take place during the spring and early summer (Walters and Yawney 1990). Seed production is prolific and good crops are produced one out of 2 years (Godman and Mattson 1976). The seedlings are shade tolerant and have moderate growth rates (Barnes and Wagner 2004). *A. saccharum* is a dominant tree in eastern North American hardwood forests and is most common in moist fertile sites, but can grow in drier sites (Barnes and Wagner 2004). Flowering and insect/wind pollination takes place during the spring, fruiting over the summer and seeds disperse in the fall (Godman et al. 1990). There is good crop production every 2–5 years (Godman et al. 1990). Seedlings are very shade tolerant and have low growth rates (Barnes and Wagner 2004). In our study

region, the northern distributional limit of these species is at around 48°N (at the −40 °C isotherm; Little 1979). Climate models under business-as-usual and reduced emission scenarios forecast declines in the abundance of these species in our study areas, except for *A. rubrum* at the northern sites where it could increase under the reduced emissions scenario (Prasad et al. 2007—ongoing). Woodall et al. (2009) have reported a shift north of the mid-latitude of the seedling layer, but Zhu et al. (2011) did not find a shift north of the leading edge; thus it is not clear if these species are already responding to current global warming.

### Environmental data

At a central location in each forest site (8 total, 4 sites × 2 latitudes), we set up environmental sensors to measure temperature and soil moisture hourly. Soil moisture (volumetric, %) data were recorded using Hobo Micro Station Data Loggers (Onset Comp. Corp.), with two sensors installed 10 cm into the soil, and air temperature was obtained at 1 m using temperature sensors/data loggers [Temperature/RH Data Logger (Onset Comp. Corp.)]. We also measured light and soil moisture each summer at each of the 120 trap–plot locations. Light at each plot was estimated using canopy photos taken once a year after the full canopy developed. Photos were taken at 1 m using a 4.5 mm fish-eye lens and processed with Hemiview software (Delta-T, Cambridge, UK) to estimate the percent of full sunlight reaching the plot. Plot-level soil moisture (volumetric, %) was measured three to five times each summer, three measurements per plot, using a Delta-T Moisture (HH2) meter. We then combined the site-level temporally intensive (hourly) and plot-level spatially extensive (15 plots per site) data to estimate the average soil moisture at each plot in each month [see Electronic Supplementary Material (ESM) 1]. Combining temporally extensive soil moisture data taken at one point with spatially extensive soil moisture data taken at each plot allowed us to reconstruct the soil moisture environment experienced by the plants at each plot during the study period. We used monthly averages of the temperature and soil moisture data and annual estimates of the light data in the analyses.

### Data analysis

We estimated the effect of the environmental conditions on the different recruitment processes following the approach used by Rollinson et al. (2016). Each recruitment process has a maximum performance value based on our 8 years of records, i.e., maximum number of seeds produced or maximum probability of transitioning to the next stage, seedlings establishing or seedlings surviving. We then estimated annual deviations from those maximums as a function of

the environmental conditions taking place each year. Here, we assume that other factors affecting recruitment (i.e., biotic factors like seed viability and predation, seedling herbivory and density dependent mortality) remained constant during the study period. Maximum performance is then modified by a Gaussian scalar, varying between zero and one, with one being the optimal value of the variable, where performance is maximized, and declining as the variable value moves away from the optimum (ESM2). The scalar for variable  $k$  at value  $i$ ,  $K_i$ , is calculated as:

$$\text{Scalar}_{k,i} = \exp\left(\frac{-0.5}{v}(K_i - m)^2\right),$$

where  $m$ , the mode, is the value of the variable at its optimum (scalar = 1) and  $v$ , the variance, is a measurement of the range of the variability in the scalar. This approach provides a large flexibility in the estimation of the effect of a variable on a process: if the variable has no effect it would result in a uniform scalar equal to one along the range of the variable; if the optimal values lie beyond the range of values included in the data, then the scalar will only show a declining or ascending trend (Canham and Thomas 2010; ESM2). We estimated scalars for several environmental variables, temperature, soil moisture and light, and also included a scalar to assess the effect of masting on seed production during the following year. We did not include interaction terms between scalars; as parameters associated with each environment variable were estimated simultaneously, estimates (and predictions from the simulations, see below) accounted for any covariance in their effects. Parameter values for  $m$  and  $v$  were estimated independently for each region, north and south, to account for regional adaptation/acclimation to local conditions. The two species were analyzed independently.

To estimate which month of the year environmental variable  $K$  is most relevant for a particular process, we weighed the effect of the variable over time by including antecedent effects (Ogle et al. 2015). If a particular process usually takes place during month  $mo$ , we then included environmental conditions during the months that could have affected that process. For example, if the preceding 2 months were included, the value of the environmental variable,  $K$ , was estimated as:  $K = \omega_{mo} \times k_{mo} + \omega_{mo-1} \times k_{mo-1} + \omega_{mo-2} \times k_{mo-2}$ , where  $k_{mo}$  are the monthly averages of the variable and  $\omega$  are the weights given to each month also estimated.

To account for observation error in our plant data (e.g., there were years where the seed counts were lower than the number of new seedlings observed and the possibility that new seedlings would have germinated after the census; see ESM3 for raw data graphs) and to link the analysis of the three data sets, seeds ( $Seeds^{observed}$ ), new seedlings ( $New\ seedlings^{observed}$ ) and older seedlings ( $Old\ seedlings^{observed}$ ), we included in the analysis the estimation of latent variables

reflecting the true number of seeds and seedlings that might have fallen, established or survived in each plot and year (latent variables  $S$ ,  $NewS$ , and  $OldS$ , Fig. 1; Lavine et al. 2002).

### Seed production

Because mast-seeding episodes may not follow all mast-flowering events (Montesinos et al. 2012), we decoupled the effects of environmental conditions that could affect seed initiation from those that could affect seed maturation (Fig. 1). We used the seed data to estimate the combined effects of environmental conditions during spring on seed initiation (flowering and pollination) and of environmental conditions during the previous summer on seed maturation (fruiting), as these would have determined the growing conditions and thus the amount of resources available for seeds (Smaill et al. 2011). The scalar accounting for the effects of spring conditions ( $SeedSpring$ ) was estimated as a function of the effects of temperature during the months of March, April and May ( $SeedSpring_t = Scalar_{temperature\ t}$ ). The scalar estimating the effects of summer conditions ( $SeedSummer$ ) was calculated as a function of temperature and soil moisture during the previous growing season (June, July and August in year  $t - 1$ ). The scalars of each of the environmental variables during the summer were multiplied for an overall value (e.g.,  $SeedSummer_t = Scalar_{temperature\ t-1} \cdot Scalar_{soil\ moisture\ t-1}$ ). To include the potential effects of masting years ( $SeedMasting$ ) on seed production the following year, we also included a scalar assessing this effect ( $SeedMasting_t = Scalar_{seedproduction\ t-1}$ ).

We considered the maximum number of seeds collected from each trap,  $p$ , during the 8-year period,  $MaxSeed_p^{observed}$ , to be a proxy for the maximum seed production potential at that plot,  $MaxS_{p,t}$ , reflecting seed sources around the plot and optimal conditions for seed production (there was no adult tree mortality around the plots, nor a significant change in the adult tree populations that could have significantly affected seed production; see ESM3 for graphs of raw data). We estimated this potential as:  $MaxS_{p,t} \sim Poisson(MaxSeed_p^{observed})$ , allowing the possibility that the maximum potential in seed production could be slightly different from what we observed. We next modeled seed production in plot  $p$  and year  $t$ ,  $Seeds_{p,t}^{observed}$ , as a function of that maximum and the effect of the environmental conditions on seed initiation and seed maturation:

$$Seeds_{p,t}^{observed} \sim Poisson(S_{p,t}),$$

$$S_{p,t} = MaxS_{p,t} \times SeedSpring_{p,t} \times SeedSummer_{p,t} \times SeedMasting_{p,t}.$$

Under optimal conditions,  $SeedSpring$  and  $SeedSummer$  would be 1, and the maximum seed production,

$MaxS$ , would only be modified by the effect of the previous year seed production. When conditions deviate from their optimum,  $SeedSpring$  and  $SeedSummer$  would be  $<1$ , and seed production for that plot and year would be reduced from its maximum potential. In earlier versions of the model, we also incorporated the effects of current year seed production, as seed density may affect predation (Ibáñez et al. 2007). However, the effects were null (scalars  $\sim 1$ ; not shown) and we removed them from the analyses to avoid overparameterization.

### Seedling establishment

Seedling establishment (seed survival to germination, establishment and seedling survival during the first few weeks) was estimated as a function of the estimated available seeds that year,  $S$ , and the environmental effects of temperature, soil moisture and light on seedling establishment (Fig. 1). As with the seed data, the effects of each environmental variable were multiplied to obtain an overall scalar modifying establishment,  $Establishment$ . The effects of temperature and soil moisture were weighed among the months of May, June and July, months when seedlings typically establish at our two study regions. We analyzed establishment using a binomial process, where the true number of new seedlings,  $NewS$ , is estimated as a function of the true number of seeds available,  $S$ , and a maximum probability of establishing (equal to one; i.e., all available seeds established) that is modified by the scalar ( $1 \times Establishment$ ). Thus, the scalar becomes our estimate of probability of establishing. We then modeled the observed new seedling data as a function of the true number of new seedlings establishing:

$$NewS_{p,t} \sim Binomial(S_{p,t}, Establishment_{p,t}),$$

$$Newseedlings_{p,t}^{observed} \sim Poisson(NewS_{p,t}).$$

### Seedling survival

Seedling survival (survival after establishment and over subsequent years) analysis was carried out as a function of seedlings available from the previous year, i.e., older seedlings ( $OldS$ ) plus established seedlings ( $NewS$ ), and of the scalars reflecting the effects of the environmental variables (Fig. 1), temperature, soil moisture and light on seedling survival ( $Survival$ ), as explained above the maximum probability of survival is one. Here again we modeled the observed data as a function of the true estimate:

$$OldS_{p,t} \sim Binomial([NewS_{p,t-1} + OldS_{p,t-1}], Survival_{p,t}),$$

$$Oldseedlings_{p,t}^{observed} \sim Poisson(OldS_{p,t}).$$



In this analysis, the antecedent effects included were temperature for the months of January to May, to account for potential effects of low temperature on winter survival. For soil moisture we included data from the growing season period between censuses, July, August and September of the previous year,  $t - 1$ , and May and June of the current year,  $t$ . Light values recorded at each plot for each year were also included in the estimation of survival ( $Survival_{p,t} = Scalar_{temperature\ t} \cdot Scalar_{soil\ moisture\ t-1} \cdot Scalar_{light\ p,t}$ ). In earlier versions of the model, we differentiated between new and older seedling survival, but parameters defining the scalars were similar and the fit of the model did not improve considerably (not shown); thus to avoid over-parameterization we did not include two separate estimates for survival.

Given the structure of the model (i.e., the inclusion of latent variables and antecedent effects), we followed a Bayesian approach in the estimation of the parameters (Clark 2005); all parameters were estimated from prior distributions with non-informative hyperparameter values. We used the software OpenBugs (Thomas et al. 2006) to estimate model parameters by running Markov chain Monte Carlo simulations. Three chains were run simultaneously for 75,000 iterations, parameters were then estimated after convergence of the chains (~20,000 iterations), thinning every 100th iteration (see ESM4 for OpenBugs code).

## Simulations

We then used parameter values estimated above to run simulations of seed production and seedling establishment and survival for each plot and year. Simulations were started with regional average values of seed production and seedling densities and were run for 8 years under the weather conditions recorded (i.e., current scenario), and under two predicted scenarios for the region (S1 and S2). S1 reflects a decline in CO<sub>2</sub> emissions (PCMB1), while S2 (GFDL A1F1) are projections based on current emissions (Handler et al. 2014). Under S1, temperatures would increase by 1.9, 0.4 and 0.7 °C in winter, spring and summer, respectively, while under the S2 the increase would be 4.6, 2.9 and 5.7 °C. Precipitation would increase by 14% in spring and 10% in the summer under S1, and it would increase by 42% in spring and decrease by 40% in the summer under S2 (Handler et al. 2014). We applied these changes to our 8-year environmental data to also simulate the year-to-year variability recorded.

Simulated changes in establishment take into consideration the simulated shifts in seed production, and changes in survival account for changes in establishment too, compounding the effects across ontogenetic stages. To minimize any effect that the initial conditions could have had on our simulations, we only report the average results for the

last 6 years. Effect sizes of the scalars [ES:  $\ln(S1/Current)$  and  $\ln(S2/Current)$ ] were estimated across all plots in each region for each year of the simulation. Effect sizes reported reflect the mean and variance of each year estimate (all plots considered) resulting in a conservative estimate of how the effects of temperature and soil moisture might change under each of the climatic scenarios tested.

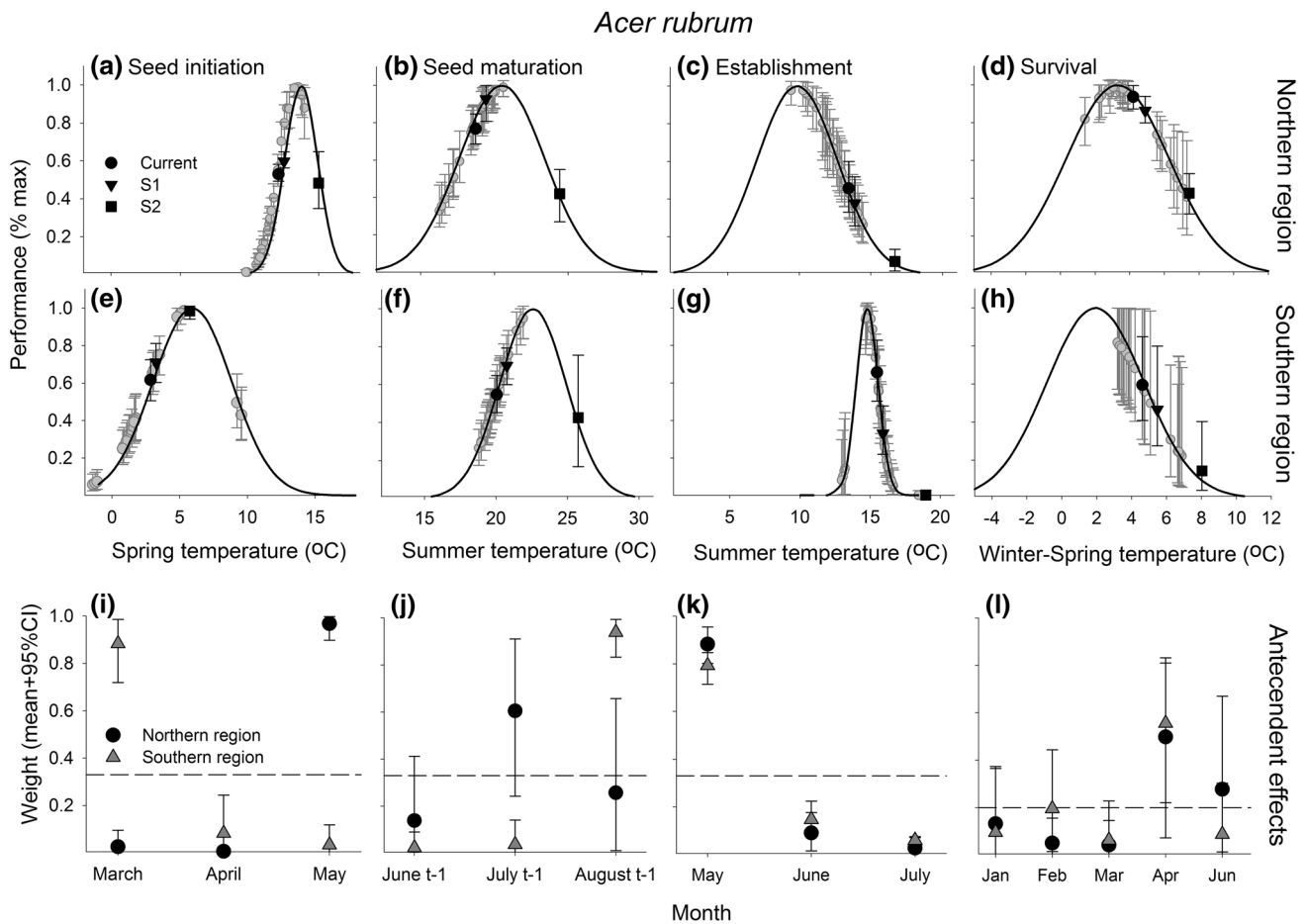
## Results

The range of weather conditions during the 8-year study period included an exceptionally warm and dry year in 2012 and a very cold year in 2014 (see ESM5 for weather data). Within a region there was a large range of spatial and temporal variability in the seed (including masting years) and seedling data for the two species. Within some plots, the densities of the two species among years fluctuated between 0 and 30 seeds/m<sup>2</sup>, 0 and 43 establishing seedlings/m<sup>2</sup> and 0 and 35 older seedlings/m<sup>2</sup>.

The fit of the models ( $R^2$ , predicted vs observed values) for *A. rubrum* were: 0.59 for the seed submodel, 0.74 for the establishment submodel and 0.88 for the seedling survival submodel. *A. saccharum* values were: 0.78, 0.61 and 0.94, respectively. Most of the effects of the environmental conditions on recruitment were driven by the temperature scalars (Figs. 2, 3). We only found marginal effects of light and soil moisture in our analyses. The scalar for light was always a flat line, ~1, except for establishment of *A. saccharum* at the northern region, where the effect peaked at ~3% of full sunlight (see ESM6 for performance curves). The scalars for soil moisture were also flat and close to the one value in most analyses except for seedling survival of *A. rubrum* in the north, where performance peaked at 60% of soil moisture (see ESM7 for parameter performance curves and antecedent effects). The effects of previous year seed production on current year seeds (*SeedMasting*) peaked between 2.7 and 4.4 seeds/m<sup>2</sup> for *A. rubrum*, and between 0.45 and 1 seeds/m<sup>2</sup> for *A. saccharum* (see ESM8 for performance curves). All parameter values are reported in ESM9.

## Seed initiation

The scalar values of spring weather affecting *A. rubrum* seed initiation were driven by May temperatures in the northern region, peaking in performance at ~14 °C, and by March temperatures in the south, peaking at ~6 °C. In both regions, the current averages are below the optimal values and scalars would increase under the two scenarios, although under S2 the scalar would fall in the descending side of the curve at the northern region (Fig. 2). In the case of seed initiation for *A. saccharum*, the scalar for



**Fig. 2** *Acer rubrum* average performance (% of maximum number of seeds or seedlings) as a function of temperature (curve), **a–d** at the northern sites and **e–h** southern sites; **a, e, i** seed initiation and **b, f, j** maturation, and seedling **c, g, k** establishment and **d, h, l** survival. *Gray symbols* represent the estimated performance (given the estimated scalar) from the data as a function of recorded temperature.

*Black symbols* represent the performance under average conditions from the data (current) and under two climatic scenarios (S1 and S2). **i–l** Antecedent effects show the weight of each month included in the analyses; *horizontal dashed line* indicates the mean of the prior values given to these parameters

spring temperature is driven by April conditions in the two regions, peaking at 6 °C in the north and at 8 °C in the south (these are weighted averages for the 3-month period). The current averages are at their peaks of their performance curves; and under the S2 scenario, scalars will decrease considerably (Fig. 3).

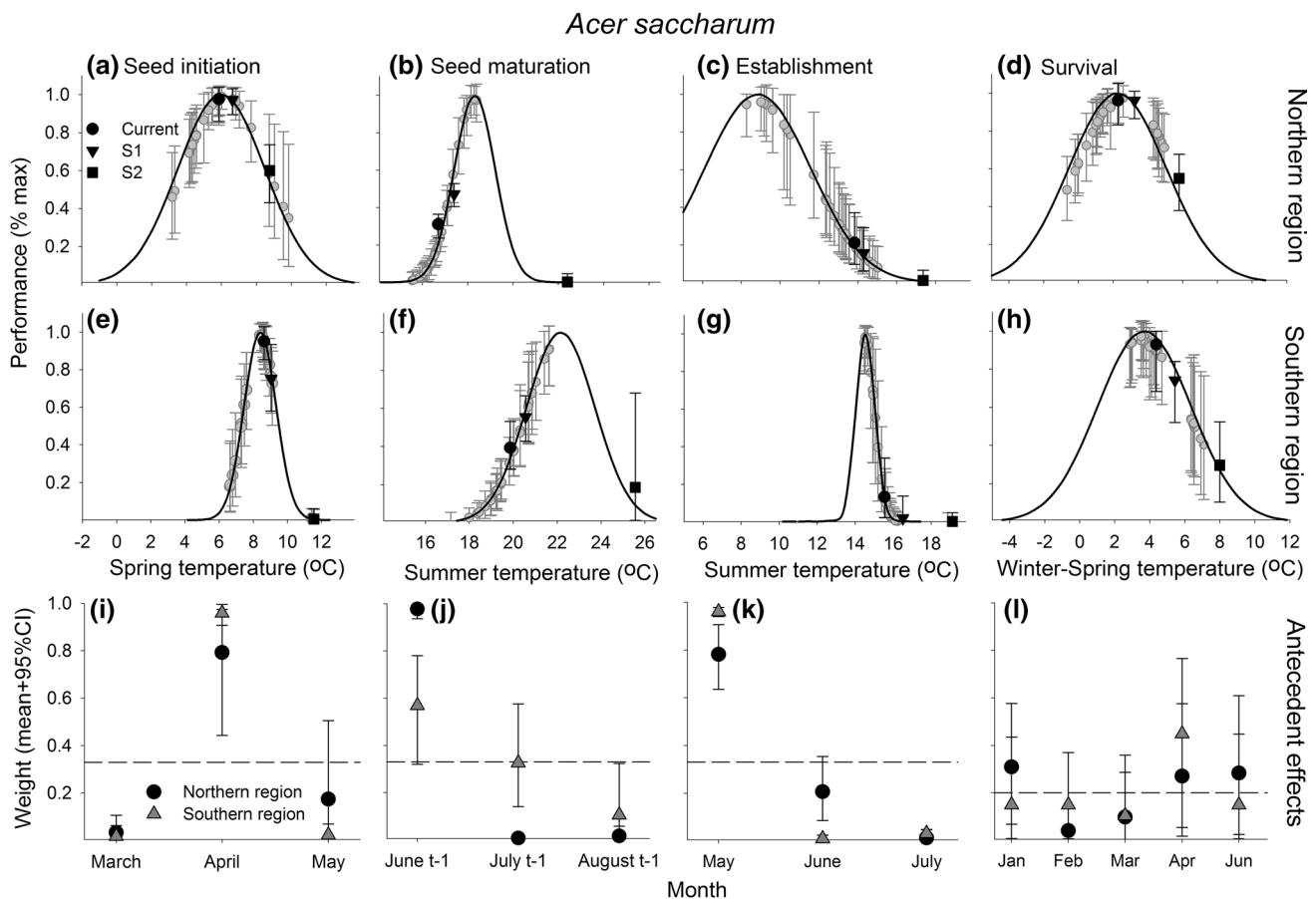
**Seed maturation**

Seed maturation of *A. rubrum* was driven by previous year July temperature in the north and strongly by August temperature in the south (Fig. 2). Maturation of seeds in *A. saccharum* was mainly affected by June temperatures of the previous year in the two regions (Fig. 3). For *A. rubrum*, the optimal temperature was similar in both regions but it varied between regions for *A. saccharum* (Figs. 2, 3). In both regions and for both species, current

averages fall on the ascending side of the scalar curve, and the value will increase under S1, but decrease under S2.

**Seedling establishment**

Establishment of the two species in both regions was mainly affected by May temperatures (Figs. 2, 3). The optimal temperature at which establishment peak varied between regions was ~10 °C in the north and ~15 °C in the south for *A. rubrum*, and ~8 °C in the north and ~14 °C in the south for *A. saccharum*. For the two species and regions, the current average conditions are associated with a scalar value past the optimal, and seedling establishment will experience further declines under the two scenarios.



**Fig. 3** *Acer saccharum* average performance (% of maximum number of seeds or seedlings) as a function of temperature (curve), **a–d** at the northern sites and **e–h** southern sites; **a, e, i** seed initiation and **b, f, j** maturation, and seedling **c, g, k** establishment and **d, h, l** survival. Gray symbols represent the estimated performance (given the estimated scalar) from the data as a function of recorded temperature.

Black symbols represent the performance under average conditions from the data (current) and under two climatic scenarios (S1 and S2). **i–l** Antecedent effects show the weight of each month included in the analyses; horizontal dashed line indicates the mean of the prior values given to these parameters

### Seedling survival

The survival temperature scalar was mainly driven by April temperature for both species and in both regions (Figs. 2, 3). Current average temperatures were near the optimal value in the north, between 3 and 4 °C for *A. rubrum* and between 2 and 3 °C for *A. saccharum*, and on the declining side of the performance curve in the south. Predicted scalars under each of the two scenarios point to a declining trend under the forecasted conditions.

### Overall recruitment

The calculated effect sizes were mostly significant for temperature effects (Figs. 4, 5). Effect sizes were mostly positive in the case of seed initiation and seed maturation, but negative for seedling establishment and survival. Overall estimates among plots and years show a slight increase in

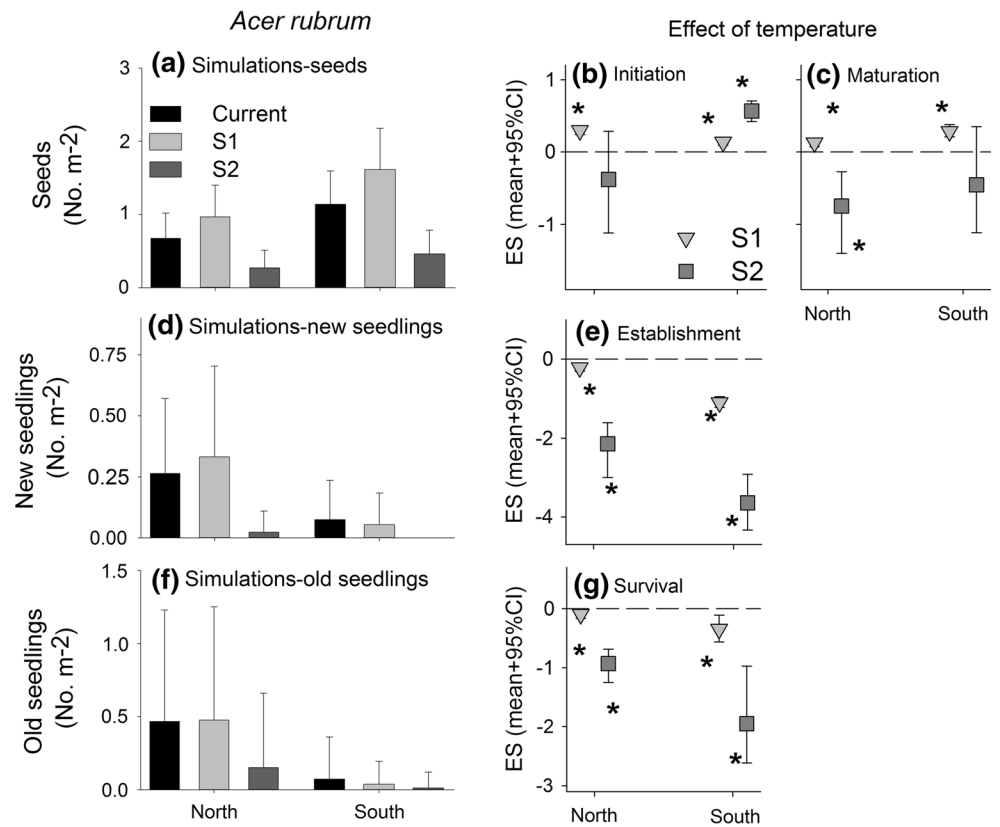
seed production, establishment and survival under S1, but strong decreases under S2 for *A. rubrum* (Fig. 4). In the case of *A. saccharum* warmer conditions could increase seed production under S1, but this would not be sufficient to compensate for the negative effects of warming conditions on establishment (new seedling estimates compound both the effects on seed production and on establishment; Fig. 5).

### Discussion

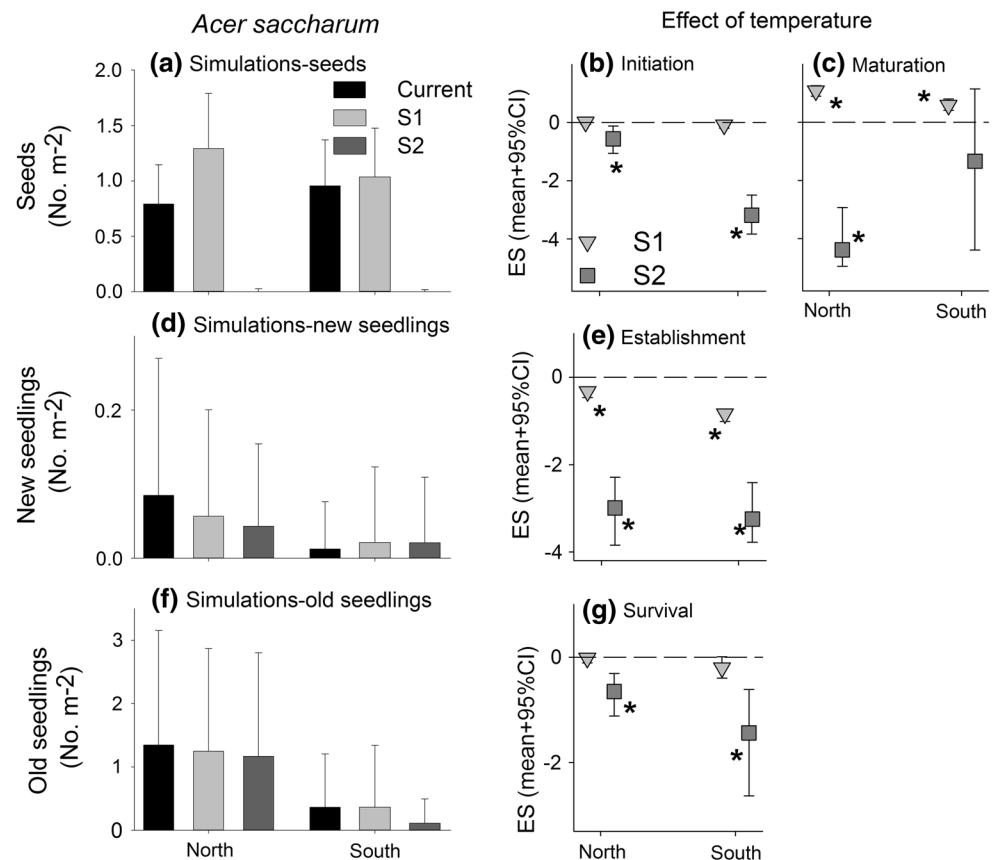
We analyzed 8 years of recruitment data to investigate how varying environmental conditions affected the processes involved in the early recruitment of two tree species. In particular, we aimed to capitalize on the observed variability in these responses to simulate targeted future responses under the projected climate scenarios for the region. Our



**Fig. 4** *A. rubrum* performance (a–c seeds, d, e new seedlings, f, g old seedlings) under the three climatic scenarios (current and the forecasted S1 and S2, both temperature and soil moisture changes were included). Simulated life stages (a, d, f) consider the density of the previous stage (seeds for new seedlings, and new seedlings for older seedlings). Effect sizes (ES, b, c, e, g) of the temperature scalars [ES:  $\ln(S1/current)$  or  $\ln(S2/current)$ ]. Asterisks indicate that ES were statistically significant, and the 95% CI around the ES does not overlap with zero. Negative values of ES indicate more detrimental conditions under the climate scenario



**Fig. 5** *A. saccharum* performance (a–c seeds, d, e new seedlings, f, g old seedlings) under the three climatic scenarios (current and the forecasted S1 and S2, both temperature and soil moisture changes were included). Simulated life stages (a, d, f) consider the density of the previous stage (seeds for new seedlings, and new seedlings for older seedlings). Effect sizes (ES, b, c, e, g) of the temperature scalars [ES:  $\ln(S1/current)$  or  $\ln(S2/current)$ ]. Asterisks indicate ES were statistically significant, the 95% CI around the ES does not overlap with zero. Negative values of ES indicate more detrimental conditions under the climate scenario



analyses show that differences exist between life stages and between populations in how trees respond to environmental cues. Annual demographic transitions were affected by the particular conditions taking place during their onset, but the effects of similar environmental shifts differed among the life stages involved in recruitment. The range of temperatures at which optimal performance took place also varied between latitudes pointing out the limitations of climate envelope models when making predictions of short-term future performance. These results also showed that similar changes in environmental conditions might have very different outcomes among populations. Our simulations of the recruitment process under two climatic scenarios revealed that the potential increase in seed production under warmer conditions may not be enough to ameliorate the negative effects of warming on seedling establishment and survival.

### **What are the environmental conditions that most influence the outcome of the different recruitment stages and at what times of the year are they most important?**

Seedling establishment and survival are two stages particularly sensitive to water availability and, for some species, also to light (e.g., Sipe and Bazzaz 1994; Weltzin et al. 2001). Therefore, we were surprised by the almost total lack of response to these two variables. We presume the effects of soil moisture may be better explained by vapor pressure deficit (VPD) than by actual soil water (we did not have reliable humidity data at all sites to estimate VPD). VPD increases exponentially with temperature (Lambers et al. 2008), strongly affecting the rates of transpiration. In our sites, the correlations between soil moisture and temperature were low ( $<0.1$ ); therefore temperature, rather than volumetric soil moisture, might have better reflected the water status of the seedlings, i.e., under similar soil moisture conditions plants will need more water at higher temperatures. The absence of a strong response to varying light levels was likely due to the shade-tolerant status of our studied species (Barnes and Wagner 2004); low light would not affect establishment and would only affect survival if light levels stayed very low over many years (Kaelke et al. 2001). The detrimental effects of increasing light on establishment of *A. saccharum* are likely due to an increased risk of desiccation which is higher under higher light exposure (Ibáñez and McCarthy-Neumann 2014).

Unlike soil moisture and light, the effects of temperature variability on seedlings recruitment were strong (Figs. 2, 3). Seed initiation in *A. rubrum* was affected by May temperature in the northern sites, but by March temperature in the south. These months coincide with the time at each region right before flowering (Ibáñez personal observation) and point to a high sensitivity of this species to the

environmental conditions leading to flowering. Seed maturation was disproportionately influenced by August conditions, but only in the south. August is one of the warmest months of the year, and at least in the southern sites high temperatures may lead to suboptimal conditions for photosynthesis if there is not enough water to compensate for the increase in evapotranspiration (Rennenberg et al. 2006). However, seed maturation of *A. saccharum* was mainly affected by temperature variability in June, the wettest month of the summer. This is a highly drought-sensitive species that likely assimilates most of its stored carbon during the wettest period of the growing season, i.e., June, when higher, rather than lower, temperatures would be closer to its photosynthetic optimum (Medlyn et al. 2002). Seedling establishment, driven by May temperatures, and seedling survival, driven by April temperatures, reached optimal values in the coldest years. During cooler springs, germinating seeds are at a lower risk of desiccating before developing a root system that can uptake water, and older seedlings may be able to optimize their carbon storage, and survive better, at their photosynthetic peak which takes place before the canopy fully develops (Kwit et al. 2010; Peltier and Ibáñez 2015).

In addition to environmental variables, temperature and soil moisture, we also estimated how seed production in a given year might have been affected by seed production in the previous year. Within each species this effect varied slightly between populations. We did not account for differential predation among years, which could be affected by seed density (Ibáñez et al. 2007; we considered this effect and did not find any indications that this could have happened at our sites) or by a masting event (lower or higher predation after masting; Nopp-Mayr et al. 2012; Schnurr et al. 2004), which we would have indirectly accounted for with our *SeedMasting* scalar. We found that effect of the previous year seed production on the current year seed output was relatively similar between regions, peaking at slightly higher seed densities at the northern site.

### **Will the different processes involved in recruitment respond differently to the same environmental change?**

Our estimates of the effects of temperature resulted in diverse performance curves among recruitment processes (Figs. 2, 3). Optimal conditions were rarely at the middle of surveyed ranges, implying that the projected increases in temperature will have different effects along the recruitment stages. Specifically, we assessed the effects of future conditions on recruitment by comparing where average conditions recorded, i.e., current scenario, and the two forecasted scenarios, S1 and S2, were on the performance curve (e.g., ascending or descending sides of the curve). As a cautionary note, for some stages, these scenarios fell beyond

the range of our data, limiting the reliability of those particular simulations, which would be entirely based on the Gaussian response we used (i.e., a modal and symmetrical response around the optimum).

Predictions for seed initiation and maturation mostly fall on the ascending side of the curves, so increasing temperatures will likely benefit these stages. Seed initiation takes place during spring, a season still relatively cold in our study region, thus warmer temperatures will likely have a positive effect on plants metabolic performance (Horvath 2009; Kumar et al. 2010). Seed maturation could also benefit under warmer conditions if these have a positive effect on the plant's capacity to store carbon, i.e., a longer growing season. However, the temperature effects will cause maturation to exceed its optimal values under S2. As we speculated above, this negative effect of higher temperature is likely linked to an increase in VPD during the hottest season, which would reduce the photosynthetic capacity and affect the amount of carbon storage by reproductive trees (Flexas and Medrano 2002).

Unlike the seed stages, optimal seedling establishment and survival seem to be already compromised. Most of the data and current and future predictions fall on the descending side of the curves (Figs. 2, 3). Warmer springs are associated with early snowmelt; thus we infer that if there is a mismatch between high moisture and seedling establishment and seedling peak photosynthetic season, these two processes would be jeopardized when the snowmelt season takes place too early.

#### **Did the populations surveyed respond similarly to the variation in environmental conditions experienced during the study period?**

In our study, we surveyed forest stands located at two different latitudes and independently assessed the effects of environmental conditions on recruitment at each location. Optimums for seed initiation in *A. rubrum* were 8 °C higher in the north than in the south, a difference mainly explained by the month driving the response (May and March, respectively). Seed maturation, however, peaked at the same temperature, 22 °C, in both regions, likely indicating the conditions during the growing season at which carbon storage is maximized (Medlyn et al. 2002). Seedling establishment also varied, with the optimum 5 °C higher in the south, indicating possible acclimation of the southern forest to higher temperatures. The optimum temperature for seedling survival was 2 °C higher at the northern sites than it was in the south. This difference might be due to a later snowmelt season in the north, where slightly warmer springs would benefit photosynthetic activity when water availability is not limited (Medlyn et al. 2002; Niinemets 2010). In the case of *A. saccharum*, we found that the same

month in each region drove the response to temperature in all the recruitment stages, but the differences in optimum temperature between regions were still considerable, 2–6 °C, except for seedling survival which was very similar in the two regions.

These disparities in optimal performance between populations point out the limitations of using species distribution data when considering recruitment dynamics under climate change. For example, establishment of *A. saccharum* seedlings peaks at 14 °C at the southern location, but performance at that temperature is less than 20% of maximum in the north (Fig. 3). Our data do not allow us to identify if these differences are due to adaptation or to acclimation of each population to the local climate. Even if it is just a transitory response due to acclimation, at least in the short-term, years to decades, the recruitment dynamics of these species will likely differ between populations, and predictions made for one location would have been a poor indicator of recruitment success at a different location.

#### **Conclusion**

Adult trees are buffered from reproductive failure during adverse years by their longevity, being able to maintain successful populations with episodic recruitment events. However, if these events decrease in frequency, at some point the population would decline. To assess the potential impact of environmental change on seedling recruitment, and ultimately better inform future forest dynamics, we can capitalize on multi-site and multi-year demographic studies that document the natural variability in the recruitment process. Predictions for our sites show that the number of seeds produced by these two species may go up as springs become warmer and growing seasons get longer, but the same changes will have a detrimental effect on establishment and survival. Higher seed production may compensate for a decrease in establishment, maintaining the number of establishing seedlings to be constant, but survival of older seedlings will decline under the predicted conditions ultimately reducing the number of recruiting seedlings. If we had only analyzed seed production, we would have forecasted an increase in the number of seeds and assumed an increase in recruitment. Focusing only on establishment or survival would have resulted in a more pessimistic outcome (ES in Figs. 4, 5). It is only when we considered the three processes that we were able to assess a likely decrease in recruitment under the predicted conditions, a decrease that also varied between regions. Therefore, as changes in environmental conditions, e.g., global warming, will have varying effects among life stages and among populations, to be able to generate more realistic forecasts of future forest dynamics we will have to consider these effects in conjunction.

**Acknowledgements** Funding was provided by the National Science Foundation (NSF) Grant (DEB 1252664) to I. Ibáñez, and by NSF-GRF and NSF-DDIG (DEB 11309805) to D. Katz.

**Author contribution statement** II conceived and designed the experiment. II, DK and BL collected data. II analyzed the data. II, DK and BL wrote the manuscript.

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