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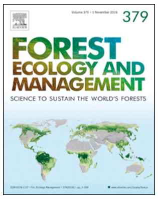

Finding the sweet spot: Shifting optimal climate for maple syrup production in North America

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ABSTRACT

Climate change is affecting the benefits society derives from forests. One such forest ecosystem service is maple syrup, which is primarily derived from *Acer saccharum* (sugar maple), currently an abundant and widespread tree species in eastern North America. Two climate sensitive components of sap affect syrup production: sugar content and sap flow. The sugar in maple sap derives from carbohydrate stores influenced by prior year growing season conditions. Sap flow is tied to freeze/thaw cycles during early spring. Predicting climate effects on syrup production thus requires integrating observations across scales and biological processes. We observed sap at 6 sugar maple stands spanning sugar maple's latitudinal range over 2–6 years to predict the role of climate variation on sugar content and sap flow. We found that the timing of sap collection advanced by 4.3 days for every 1 °C increase in March mean temperature, sap volume peaked at a January-May mean temperature of 1 °C, and sap sugar content declined by 0.1 °Brix for every 1 °C increase in previous May-October mean temperature. Using these empirical relationships, we projected that the sap collection season midpoint will be 1 month earlier and sap sugar content will decline by 0.7 °Brix across sugar maple's range by the year 2100 in an RCP 8.5 climate change scenario. The region of maximum sap flow is expected to shift northward by 400 km, from near the 43rd parallel to the 48th parallel by 2100. Our findings suggest climate change will have profound effects on syrup yield across most of sugar maple's range; drastic shifts in the timing of the tapping season accompanied by flat to moderate increases in syrup yield per tap in Canada contrast with declines in syrup yield and higher frequencies of poor syrup production years across most of the U.S. range.

1. Introduction/Background

Over the past six decades, ecosystems have experienced changes in average climate conditions including multi-decadal warming, increased inter-annual variability of surface temperatures, and changes in average precipitation (IPCC, 2014). Climate change trends are influencing how humans interact with ecosystems, including the procuring of natural resources for societal use. For example, increased climatic variability and extreme weather conditions have altered the productivity and geographic range of many plant species that provide forest products and agricultural crops (Ray et al., 2015). These changes have resulted in shifts in crop yields, crop quality, farmer livelihoods, and overall management practices (Hertel et al., 2010; Ahmed et al., 2014). While the focus of a large portion of agricultural research involving climate impacts has been on annual crops (e.g. Rosenzweig et al., 2014), perennial crops face distinct and significant challenges (Lobell et al., 2006; Lobell and Field, 2011; Lobell et al., 2011; Rosenzweig et al., 2014; Wolfe et al., 2018) yet receive little attention.

Sap procured from several species within the genus *Acer* is used to make maple syrup and is an example of a perennial plant-based forest resource that is experiencing variation in productivity due to climate change (Duchesne et al., 2009; Skinner et al., 2010; Houle et al., 2015; Matthews and Iverson, 2017). The collection of maple sap for the production of syrup and sugar is an important traditional practice,

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cultural mainstay, and commercial activity for local economies and forest management throughout the maple range of eastern North America (Keller, 1989; Hinrichs, 1998; Whitney and Upmeyer, 2004; Murphy et al., 2012). Most sap used for syrup production is collected from natural forest stands of sugar maple, *Acer saccharum* Marsh. Maple syrup production has been increasing approximately 10% per year in the United States for the past decade (National Agricultural Statistics Service, 2017) with stable high prices (McConnell and Graham, 2016) largely held in place due to market concentration and supply management in Quebec (Farrell and Chabot, 2011; Farrell, 2013). The industry supports thousands of producers and provides permanent and seasonal income streams to local farmsteads and indigenous communities who have historically used maple as a food source and in trade (Murphy et al., 2012).

Inter-annual climate variability across the range of sugar maple has raised concerns about the impact of climate fluctuations and warming trends on the maple syrup industry (Galford et al., 2014; Melillo et al., 2014), but models have thus far been limited to just a portion of sugar maple's geographic range and have not simultaneously accounted for climate effects on sap flow and the sugar content of sap (Duchesne et al., 2009; Guilbert et al., 2014; Houle et al., 2015; Skinner et al., 2010). Maple sap flows during the late winter and early spring in North America, when temperatures swing below and above freezing and generate pressure differentials within maple xylem tissue, resulting in sap exudation (Tyree, 1983; Ceseri and Stockie, 2013; Graf et al., 2015). The physical mechanism of sap flow relies primarily on temperature fluctuations, which are closely tied to inter-annual climate variability (Fig. 1). Thus, the timing of maple sap flow, as well as total yield are anticipated to respond to climate changes occurring across sugar maple's range (Duchesne et al., 2009; Skinner et al., 2010; Guilbert et al., 2014; Houle et al., 2015).

The sugar content of sap is derived from nonstructural carbohydrates stored by trees during prior growing seasons (Muhr et al., 2016). The balance of photosynthesis and respiration drive carbohydrate storage in trees (Kozlowski, 1992), with respiration increasing faster with temperature than photosynthesis at typical growing season temperatures in sugar maple (Gunderson et al., 2000). Prior work has shown correlations between sap flow and sap sugar concentrations with daily temperatures (Pothier, 1995), and syrup production with regional climate (Houle et al., 2015), but no study has projected future sap flow, sap sugar concentration, and syrup production from site-scale empirical data correlated with climate across the range of sugar maple.

Here we address this knowledge gap by constructing a statistical model of sap flow and sugar content as informed by a unique set of standardized empirical observations. We expect both tapping season and prior summer climate to impact maple syrup production via effects on sap flow and sugar content. Specifically, we predict sap flow to be influenced primarily by mean temperatures during the tapping season, while we expect sugar content in sap to be influenced more by temperature and precipitation in the prior summer, by affecting carbon storage via the balance of respiration and photosynthesis. We therefore test whether and how monthly and season-long average temperature during the tapping season (January – May across our network) and temperature and precipitation during the previous growing season (May – October) affect sap flow and sugar content from individual trees, following a standardized sap sampling protocol across multiple harvest seasons at 6 intensively sampled sites (Table 1). We focus on monthly average climate because forecasts of monthly and seasonal climate are more reliable over both near term (i.e. sub-seasonal and seasonal forecasts) and long-term (by the end of the century) timescales compared to daily freeze-thaw cycles that drive sap flow on a daily scale. Most CMIP3 and CMIP5 models underestimate the daily temperature range (Thrasher et al., 2012; Sillmann et al., 2013), with downscaling often resulting in modeled minimum temperatures greater than modeled maximum temperatures (Lindvall and Svensson, 2015). Finally, using future projections of mean temperatures for our sites, we construct estimates for sap flow, sugar content, and syrup production through the year 2100 and thus generate findings in a context useful to syrup producers, trade-groups, land managers, and policy makers when planning investments or policies related to syrup production in the region.

2. Methods

2.1. Data collection

Study sites. Sampling was carried out at six sites distributed across the geographic range of sugar maple (*Acer saccharum*) in North America. Sites ranged from southwest Virginia in the United States to Chicoutimi in the Canadian Province of Quebec at the northern range limit of sugar maple, and from Massachusetts in the east to Indiana in the west (see Table 1). Ownership of the sites range from public (Indiana Dunes National Lakeshore), to institutional (Dartmouth Organic Farm, Harvard Forest) and private enterprise (Virginia, Quebec), and each site had been previously used for maple sap collection. These sites are part of the ACERnet (*Acer* Climate and Socio-Ecological Research Network), which was formed in 2014 to investigate the impacts of climate variability on the maple socio-ecological system through

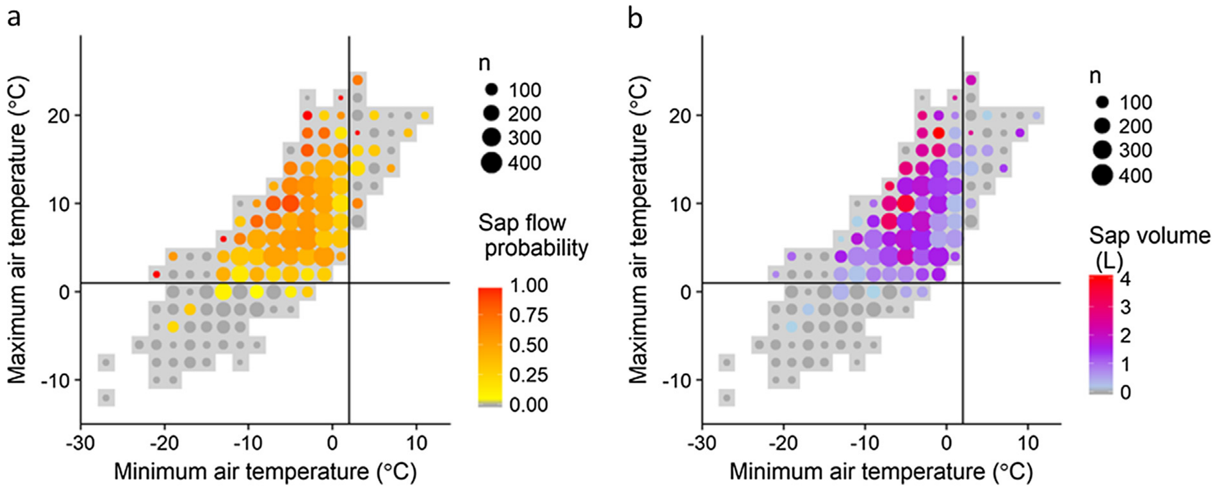

Fig. 1. (a) Sap flow probability and the (b) average amount of sap collected per tap as related to minimum and maximum daily air temperature. Vertical lines at 1.5 °C and horizontal lines at 1.0 °C indicate the modeled optimal minimum and maximum temperature thresholds.

Table 1
Description of sites used in this study.

Site	Location	Latitude	Longitude	No. of trees	Year initiated
Divide Ridge	Southwest Virginia	37.011	−82.676	15	2016
Southernmost Maple	Central Virginia	38.231	−79.658	15	2014
Indiana Dunes National Lakeshore	Indiana	41.625	−87.081	24	2016
Harvard Forest	Massachusetts	42.532	−72.190	19	2012
Dartmouth Organic Farm	New Hampshire	43.734	−72.249	25	2014
Quebec – Northern range	Quebec	48.431	−70.688	20	2014

analysis of sap yield, sugar content, and secondary compounds as well as through producer surveys. These sites span the range of sugar maple and the temperature conditions under which it grows, and the individual years sampled provided good coverage of the climates experienced by individual sites (Fig. S1.)

Field data collection. At each site, we collected xylem sap measurements from between 15 and 25 mature sugar maple trees throughout the sap flow season. We defined a collection day as one in which a commercial maple syrup producer would collect for the process of boiling to make syrup; generally, this referred to when at least one liter of sap accumulated per tap. If a smaller amount of sap flowed, it was left in the collection device (a bucket or plastic sap bag) until the next collection day so that all sap flow during the season was measured. Collections varied by site and ranged from January (Virginia) through to early May (Quebec).

Sap from mature trees was collected using traditional gravity tapping methods following accepted maple tapping guidelines for gravity tapping (Heiligmann et al., 2006). Only trees > 12″ (30.5 cm) DBH (diameter at breast height) were tapped. Trees < 20″ (50.8 cm) DBH received one tap, while trees > 20″ (50.8 cm) DBH received two taps. The first year a tree was tapped, we chose a random bearing of 0–360°, and a random height of 80–160 cm for the first tap to avoid a systematic bias in tap orientation. For trees with a second tap, the tap was placed at 180° from first tap and at same height. In subsequent years, to avoid tapping into wood damaged by previous tapping, tap holes were placed 4″ (10 cm) to the right, and 6″ (15 cm) above the previous year's hole, unless the previous year's hole was at a height greater than 145 cm. In that case, the tap was placed at 80 cm above ground. Trees were tapped with 5/16″ spiles inserted into holes drilled at a slight (~10°) upward angle, no more than 2″ (5 cm) into the wood.

For each sap collection for each tap, the weight of sap in kilograms was recorded using a Pelouze 50 lb./22.5 kg Capacity Electronic Hanging Scale (Rubbermaid, Huntersville, NC). The sugar content of sap collected directly from each tap was measured in °Brix (percent sucrose by mass) using a Misco Palm Abbe Digital Refractometer (MISCO, Cleveland OH). In addition to sap weight and sugar content, we noted additional information regarding tap conditions in the event of a collection malfunction (e.g., leak in the sap bag) so as to identify potential sources of error in our data.

Climate data. We used Daymet climate data to characterize climate across our study sites. Daymet is a gridded climate data product of daily weather parameters interpolated and extrapolated from daily ground-based meteorological observations (Thornton et al., 1997; Thornton et al., 2017). The Daymet dataset spans the study region and therefore provided a consistent set of climate variables with which to compare sites as well as to construct relationships between sap flow and general climate. In addition, the 1 km by 1 km grid size approximates the spatial footprint of individual sap collection sites. We therefore expect the spatial heterogeneity of climate within our study sites to approximate that within Daymet grid cells. For each of our sites, we identified the Daymet grid cell that contained our sampling area and collected daily minimum and maximum temperature for 1980–2017. Using this information, we calculated daily mean temperature as $(T_{max} + T_{min})/2$. To calculate monthly mean temperature, we then took the mean of our calculated daily mean values. We took the mean of monthly values to calculate season-long mean temperature and precipitation.

2.2. Data analysis

Sap data. Since some trees had two taps, we first calculated the mean sap weight per tap (kg) and the weighted (by sap weight) mean of sap sugar content per tap (°Brix) for each tree on each day of each tapping season at each site. We calculated a weighted mean for sap sugar content because different taps of the same tree can sometimes have very different flow volumes on a given day. For trees that were missing data on certain dates, we used a linear mixed model approach implemented with the lme4 package version 1.1–1.5 (Bates et al., 2015) in R version 3.4.3 (R Core Team, 2017) to predict sap sugar and sap weight for those dates. For both measures, we modeled date (as a factor) as a fixed effect and tree as a random effect using data from just the site and year of interest.

From these daily data, we calculated metrics for (1) tapping season timing, (2) sap volume, and (3) sap sugar content. While tapping date is subjectively decided by the producer, climate conditions dictate the timing and quantity of sap flow once tapping has occurred. To describe the dynamics of sap flow timing, we identified the dates when 10%, 50% and 90% of the sap collected for the season occurred for each tree at each site. We calculated the length of the sap collection season by counting the number of sap collection days between the dates when 10% and 90% of sap was collected from each tree. Finally, for each tree we calculated total sap volume collected over the entire tapping season (L/tap) as the sum of daily sap volume and the mean sap sugar (°Brix) as the weighted (by sap volume) mean of daily sap sugar content values over the entire tapping season. We then estimated the total amount of syrup for each tree that could be produced from the sap collected, assuming that maple syrup contains 0.8833 kg of sugar per liter (US Department of Agriculture, 2015), using the formula:

$$Syrup\ (L/tap) = sap\ weight\,(kg/tap) * sap\ sugar\,(°Brix)/100(\%)\,/0.8833(kg\ sugar/L\ sap) \quad (1)$$

Understanding optimal periods for tapping and sap flow required investigating how sap flow dynamics related to freeze/thaw cycles (sensu Skinner et al., 2010; Guilbert et al., 2014). We constructed metrics for predicted timing and the total number of freeze-thaw days from daily minimum and maximum temperatures, then compared them to our sap collection data. We first tested thresholds for minimum and maximum daily temperatures that best predicted whether sap collection would occur. We assigned each day within the tapping season (from first sap collection to last sap collection for each year at each site) as a day that either: (a) contained a freeze/thaw cycle and therefore likely to support sap flow, (b) was too warm for sap flow, or (c) was too cold for sap flow. We considered a freeze/thaw cycle to have occurred on a day when the minimum temperature was below the freezing threshold and the maximum temperature was above the thawing threshold. If the minimum temperature was above the freezing threshold, we considered the day too warm for sap flow, while if the maximum temperature was below the thawing threshold, we considered it too cold for sap flow.

We considered temperatures for both freezing and thawing thresholds of every half degree between −3 °C and 3 °C and used binomial

Table 2

Summary of statistical tests comparing freeze-thaw cycles, sap collection, and climate. The models shown are those for which the AICc weight for each model set was at least 0.05. The best model for each model set as determined by AICc is italicized. *Used for projections.

Response	Predictor	Random	Model	df	dAICc	AICc weights	intercept	beta0	beta1	R^2 (marginal)
Timing, collections	*Timing, freeze-thaw*	*Site:Year*	*Quadratic*	*5*	*0.00*	*0.99*	*73.66 ± 13.95*	*−0.84 ± 0.42*	*0.011 ± 0.003*	*0.76*
Sap collections	*Freeze-thaw cycles*	*Site:Year*	*linear*	*4*	*0.00*	*0.68*	*−20.78 ± 10.91*	*0.96 ± 0.34*		*0.27*
Sap collections	Freeze-thaw cycles	Site:Year	Quadratic	5	1.80	0.28	10.29 ± 1.08	62.38 ± 18.21	10.76 ± 21.30	0.27
Timing, freeze-thaw	*January-May temp*	*Site*	*Quadratic*	*5*	*0.00*	*1.00*	73.10 ± 1.26	−317.57 ± 17.89	−81.72 ± 16.09	*0.75*
**Timing, collections*	*January-May temp*	*Site:Year*	*Quadratic*	*5*	*0.00*	*0.52*	87.77 ± 1.90	−4.34 ± 0.31	−0.09 ± 0.06	*0.86*
Timing, collections	January-May temp	Site:Year	linear	4	0.17	0.48	85.95 ± 1.45	−4.47 ± 0.31		0.86
Freeze-thaw cycles	*February temp*	*Site*	*linear*	*4*	*0.00*	*0.61*	*35.58 ± 1.39*	*0.28 ± 0.08*		*0.10*
Freeze-thaw cycles	February temp	Site	Quadratic	5	1.74	0.26	34.42 ± 1.34	23.73 ± 6.95	−2.61 ± 4.52	0.11
Sap collections	*January-May temp*	*Site:Year*	*Quadratic*	*5*	*0.00*	*0.85*	*10.58 ± 0.89*	*−6.63 ± 17.27*	*−76.73 ± 16.87*	*0.44*
Sap collections	April temperature	Site:Year	Quadratic	5	5.30	0.06	10.58 ± 0.93	−19.01 ± 18.03	−62.78 ± 17.67	0.35
**Total sap*	*January-May temp*	*Site:Year*	*Quadratic*	*5*	*0.00*	*0.41*	*42.84 ± 6.15*	*92.61 ± 85.38*	*−246.16 ± 84.51*	*0.23*
Total sap	April temperature	Site:Year	Quadratic	5	2.40	0.12	42.76 ± 6.50	53.86 ± 89.79	−218.70 ± 88.86	0.17
Total sap	January temp	Site:Year	Quadratic	5	2.93	0.09	42.56 ± 6.57	99.31 ± 91.03	−194.28 ± 87.09	0.16
Total sap	February temp	Site:Year	Quadratic	5	2.98	0.09	42.51 ± 6.56	75.52 ± 91.86	−205.78 ± 90.60	0.16
Total sap	March temperature	Site:Year	Quadratic	5	3.45	0.07	42.10 ± 6.63	95.29 ± 92.33	−191.98 ± 93.69	0.15
Total sap	May temperature	Site:Year	Quadratic	5	4.15	0.05	42.27 ± 6.74	66.64 ± 95.10	−186.39 ± 94.12	0.13
**Sap sugar*	*Prior May-October temperature*	*Site:Year*	*linear*	*4*	*0.00*	*0.19*	*4.29 ± 0.48*	*−0.12 ± 0.03*		*0.19*
Sap sugar	Prior May-October temperature	Site:Year	Quadratic	5	0.27	0.17	2.39 ± 0.06	−3.48 ± 0.86	−1.12 ± 0.87	0.21
Sap sugar	Prior September temp	Site:Year	linear	4	0.29	0.16	3.85 ± 0.38	−0.09 ± 0.02		0.19
Sap sugar	Prior September temp	Site:Year	Quadratic	5	1.48	0.09	2.39 ± 0.06	−3.47 ± 0.89	−0.81 ± 0.89	0.20
Sap sugar	Prior May temp	Site:Year	linear	4	2.03	0.07	3.78 ± 0.39	−0.10 ± 0.03		0.17
Sap sugar	Prior May temp	Site:Year	Quadratic	5	2.11	0.07	2.39 ± 0.06	−3.19 ± 0.87	−1.14 ± 0.85	0.18
Sap sugar	Prior October temp	Site:Year	linear	4	2.26	0.06	3.21 ± 0.24	−0.09 ± 0.02		0.16

regression to model whether sap was collected as a function of temperature domain for each threshold pair. We statistically considered the thresholds used in the model with the lowest AICc (Burnham & Anderson, 2002) as those that best predicted sap flow. Using these thresholds and data on the density of sap collection days during the tapping season, we determined the optimal timing for sap flow based on the density of daily freeze/thaw cycles. Our data on sap collection days revealed that 95% of sap collection seasons were 45 days or less, and that sap collections were uniformly distributed during the season (Kolmogorov-Smirnov test; of the 387 tree/years tested, less than 5% had a $p < 0.05$ and the modal p-value was 1, Fig. S2). While our sap collections occurred from mid-winter through spring, we calculated the period with the most freeze/thaw events in a 45-day period between October 1 and May 31 to examine the entire potential freeze-thaw season. The daily probability of a freeze/thaw cycle generally had two peaks during this period, with the spring peak being taller and sharper than the fall peak at all sites (Fig. S3), and a minimum in early- to mid-January. We therefore further constrained the optimal period for freeze/thaw to occur after January 1, which coincides with our sap collection data. We took the median date of the optimal period for freeze/thaw cycles as a measure of the timing for the optimal potential sap flow season. Finally, we counted the number of freeze/thaw cycles of this window of time as a measure of the potential sap flow days. This approach provided a calculated optimal window for sap flow and a total count of the potential sap flow days for each site in each year.

We used regression analyses to examine relationships between the optimal period of sap flow predicted by the occurrence of freeze/thaw cycles, actual sap collection, and monthly climate. Specific comparisons are shown in Supplementary Tables S1–S3. We tested whether the occurrence of freeze/thaw cycles predicted actual sap collection, and whether climate predicted both the occurrence of freeze/thaw cycles and actual sap collection. Since the maple tapping season begins in January at our southernmost site and ends in May at our northernmost site, we fit models with mean monthly temperatures for all months of the network-wide tapping season and season-long (January – May) mean temperature as predictors for the timing of freeze/thaw cycles and sap collections, number freeze/thaw cycles and sap collection days, and total sap collected. Likewise, to predict sap sugar content, we fit models with previous growing season (May – October) mean monthly temperatures and precipitation, as well as mean season-long temperature and precipitation as predictors. We hypothesized that growing season temperature would influence carbohydrate storage via inhibitive effects on photosynthesis during the hottest part of the day and nighttime respiration rates (Kozlowski, 1992). Mixed model linear and quadratic regressions were performed for all comparisons implemented with the lme4 package version 1.1–1.5 (Bates et al., 2015) in R version 3.4.3 (R Development Core Team, 2017). Multiple trees were tapped at each site, over multiple years; we therefore included the site by year combination as a random effect in all models that tested sap collection data to avoid pseudo-replication. Models in which the response variable was a freeze/thaw cycle-derived metric had one data point per site per year; in this case site alone was included as a random effect. We compared the NULL model (random effects only), linear regression, and quadratic regression for each predictor using AICc (Burnham and Anderson, 2002). We used AICc to choose the best fitting model for projections (see below), although in some cases competing models were nearly as good. We also report marginal R^2 values (Nakagawa and Schielzeth, 2013; Barton, 2018) to evaluate the strength of the relationship. Marginal R^2 represents the amount of variance explained by the fixed effects portion of the model (Nakagawa and Schielzeth, 2013), and is therefore indicative of the variance we would expect to explain using these relationships to predict sap collection at other sites, as in projections (see below).

In order to validate the relationships used for projective modeling, we randomly sampled half of the trees per site, and used this dataset to test relationships between tapping season mean monthly temperatures and both the midpoint of the sap collection season and total sap collected, as well as previous growing season mean monthly temperatures and sap sugar concentration. We then calculated population means for each site and year using data from the remaining trees, and predicted population means for each site and year using just the fixed effects of the models. This allowed us to compare predictions to observations at the scale of the planned projections. We calculated the Nash and Sutcliffe efficiency coefficient (Nash and Sutcliffe, 1970) between

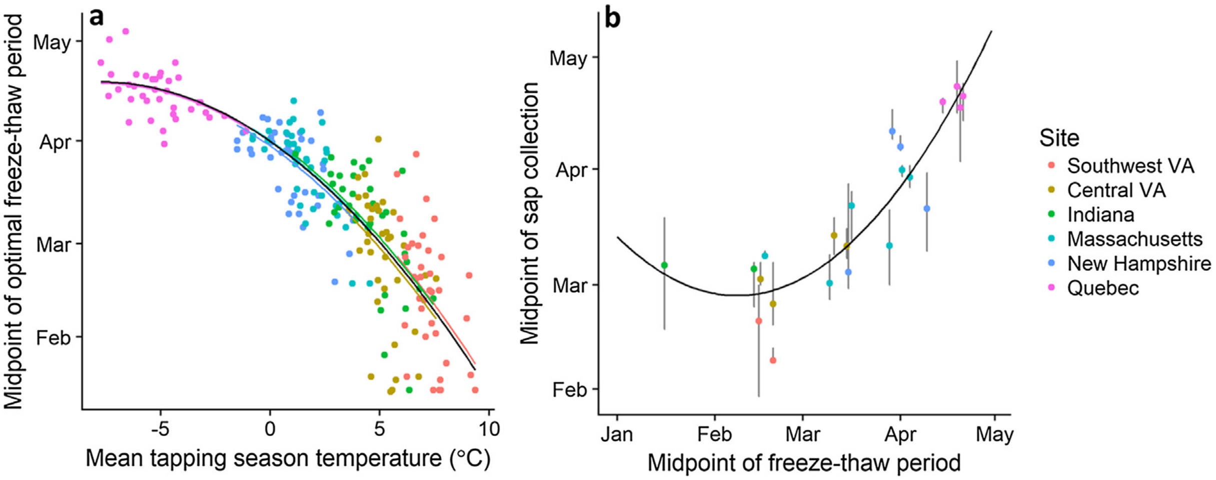

Fig. 2. (a) Mean tapping season (January-May) temperature was a significant predictor for the timing of the period with the maximum number of freeze/thaw days, while (b) the optimal period for freeze/thaw cycles predicted the midpoint of the sap collection season. Points represent means for each site in each year of sampling, while vertical bars depict the range of values observed across trees within each site and year.

predicted and observed values and conducted a paired *t*-test comparing these values to provide a gauge of model performance.

2.2.1. Projections of future sap and syrup dynamics

We used the empirical relationships between climate and sap collection data to project future tapping season timing, sap volume, sap sugar content, and potential syrup produced on a per tap basis for our study sites using historical climate data and future climate projections. Additionally, we used historical data and future projections of monthly temperature to project past and future tapping season timing, total sap volume, and sap sugar content per tap using coefficients from the models that best fit our empirical data (see Results, Table 2). We then calculated projected total syrup production per tap from projected total sap volume per tap and projected sap sugar content using the formula above.

In order to construct a baseline for comparison, we used historical climate data to simulate past trends of sap dynamics at our sites. We used monthly mean temperature data reported on an 1/8°grid for North America for 1950–1999 by Maurer et al. (2002) and Daymet data for the period 1980–2017. For overlapping years, we took the mean of monthly temperatures of the two datasets as our input data. For projected future climate, we chose 14 statistically downscaled models (the CMIP5 multi-model ensemble dataset) recommended for use for climate impact studies in the northeastern US (Table S4; Karmalkar et al., 2019). For each climate simulation, we downloaded the first model run of the RCP 8.5 emissions scenario (IPCC, 2014) for models with multiple runs available from the Bureau of Reclamation data portal (Reclamation, 2013). We chose RCP 8.5 because it follows most closely current trends in global carbon emissions (USGCRP, 2017). To gain a broader perspective of potential changes to sap and syrup dynamics throughout the range of sugar maple's distribution, we also projected these variables for each grid cell of the climate projection within the geographic area bounded by longitudes −95.0625 and −67.0625 and latitudes 36.4375 and 49.9375, which contains most of sugar maple's native distribution (Little, 1971). Finally, to explore the frequency of favorable production years over historical and projected future periods, we calculated the percent of years that exceeded traditional thresholds of production. Traditionally, the sap to syrup ratio was considered to be 40:1, which implies a sap sugar concentration of 2.2 °Brix; a good crop was expected to be ~1L of syrup per tap.

For future projections, we calculated the mean and 95% prediction interval over all models for each parameter to estimate extreme high and low years over time. Both the mean and 95% prediction intervals were smoothed using locally-weighted scatterplot smoothing (LOWESS; Cleveland, 1981). For the range-wide analysis, we estimated mean over the years 1950–1999 (N = 50) for historical data and compared this to the projections for the period 2090–2099, calculating the mean over models and years (N = 140 model years). For both periods, we also calculated the frequency of years that exceed traditional thresholds of production: sap production of 40 L/tap, sap sugar content of 2.2 °Brix, syrup production of 1 L/tap, and sap collection season midpoint of March 1. Finally, we calculated the absolute difference between 1950–1999 and 2090–2099 for both mean values and the frequency of years that exceeded these traditional thresholds of production.

3. Results

3.1. Effects of temperature on syrup production parameters

The freeze/thaw thresholds that best predicted sap collection data at our sites were a minimum temperature equal to or below 1.5 °C and a maximum temperature equal to or above 1.0 °C (binomial model with the lowest AICc; Fig. S3). Using this definition of a freeze/thaw cycle, we calculated that sap was collected on 46.7% of days with a freeze/thaw cycle (95% CI: 45.8–47.6%), 18.3% of days that were above freezing (95% CI: 16.3–20.5%), and 3.2% of days that were below freezing (95% CI: 2.6–3.9%). However, we noted that when minimum air temperature was at or below −8.0 °C, total sap collected was usually lower and when maximum temperatures were at or above 5.0 °C, there was sometimes flow even when minimum air temperatures did not go below 1.5 °C (Fig. 1). This may be attributed to sap flow that continued following our collections due to a freeze/thaw cycle one day prior or to within-stand temperature fluctuations not captured by the coarser climate data.

From a broad climate perspective, the timing of the freeze/thaw period (Table 2; Fig. 2a) was best explained by season-long (January – May) tapping season temperature in a negative but non-linear way. Much of the unexplained variance in the timing of the optimal freeze-thaw period was for sites and years at the higher end of mean tapping season temperature, indicating that warmer springs make anticipating the optimal freeze/thaw period based on average temperature more challenging. This may be why the relationship between the midpoint of the period of maximum freeze/thaw days and the timing of the middle of the sap collection season (day on which 50% of sap was collected) was not linear (Table 2; Fig. 2b). For years in which the optimal period for freeze/thaw cycles was after mid-February, the slope was approximately 1 but for years with earlier optimal freeze/thaw periods the slope approached 0, possibly indicating a mismatch between when trees

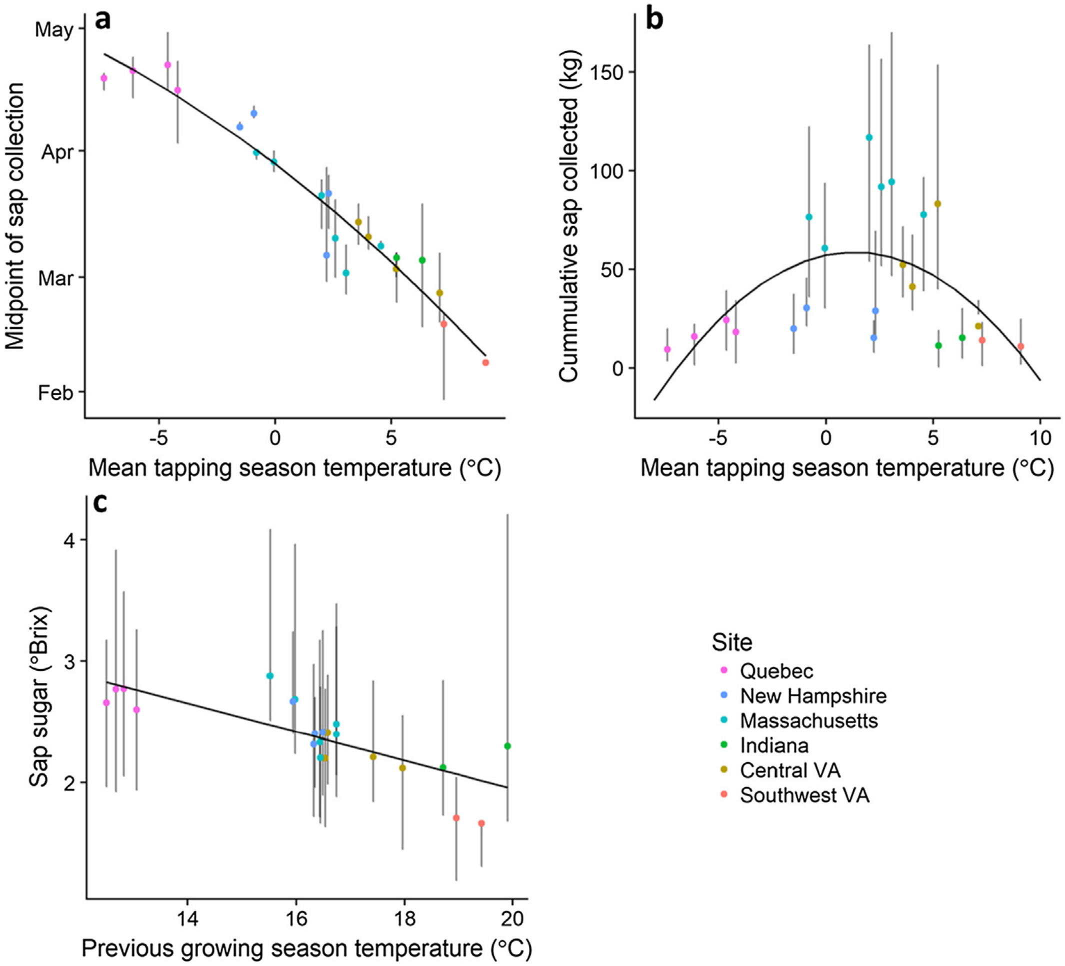

Fig. 3. Tapping season metrics are predicted by monthly mean climate. (a) Mean tapping season (January – May) temperature predicts the date when 50% of sap is collected. (b) Total season sap collected per tap had a hump-shaped relationship with mean tapping season temperature. (c) Sap sugar concentration had a negative relationship with previous growing season (May – October) mean temperature. Points represent means for each site in each year of sampling, while vertical lines depict the range of values observed across trees within each site and year.

were tapped and the optimal freeze/thaw period. However, the midpoint of the sap collection period was tightly predicted by mean January-May temperature (Table 2; Fig. 3a), with sap collection occurring earlier when mean temperature was higher. Tapping season temperature explained much more of the variance in the timing of sap collections than it did for the timing of the optimal freeze/thaw period. The mean timing of the midpoint of the tapping season calculated from trees not included in developing the regression relationship was not different from the predicted population mean ($t = 0.3011$, $df = 21$, $p = 0.7663$) and the predicted relationship explained most of the variation in the calculated population mean (Efficiency = 0.92).

Mean tapping season temperature was a significant predictor in the quadratic regression for the season long number of total sap collections, although February temperature was a better predictor of the number of freeze/thaw days (Table 2). However, the number of sap collection days was linearly related to the number of freeze-thaw days in the optimal freeze/thaw period (Table 2).

Mean tapping season temperature was the best predictor of total sap volume, although the relationship with individual month mean temperatures for each individual tapping season month (January – May) were nearly as good (Table 2). The quadratic regression between total sap volume and mean tapping season temperature (Fig. 3b) was similar to the relationship with number of sap collection days, although the variance explained was lower. The mean total sap collected from trees not included in developing the regression relationship was not different from the predicted population mean ($t = 0.173$, $df = 21$, $p = 0.8643$) and the predicted relationship explained about a third of the variation in the calculated population mean (Efficiency = 0.30).

Finally, sap sugar concentration was negatively and linearly related to the previous growing season temperature (Fig. 3c), although the quadratic regression was nearly as good, as were regressions involving May, September, and October mean temperatures (Table 2), with the trend of the relationship being similar for all predictors. Precipitation had much less predictive power than temperature, with delta AICc values greater than 7 for all models (Table S3). The mean sap sugar concentration of trees not included in developing the regression relationship was not different from the predicted population mean ($t = 0.3229$, $df = 21$, $p = 0.75$) and almost half of the variation in the calculated population mean was explained by the predicted relationship (Efficiency = 0.48).

3.2. *Reconstructing historical and projecting future tapping seasons*

Linear regression of hindcasted sap variables at individual sites revealed that the Massachusetts and New Hampshire sites were the only locations where the mean value of any sap variable changed over the period 1950–2016. For the New Hampshire site, modeled tapping season midpoint ($slope = -0.1127$, $F(1,64) = 11.5$, $p = 0.0012$, $R^2 = 0.14$), sap sugar content ($slope = -0.0033$, $F(1,64) = 54.64$, $p < 0.0001$, $R^2 = 0.45$) and total syrup volume ($slope = -0.0018$, $F(1,65) = 13.86$, $p = 0.0004$, $R^2 = 0.17$) declined over time using our model. For the Massachusetts site, only total syrup ($slope = -0.0010$, F

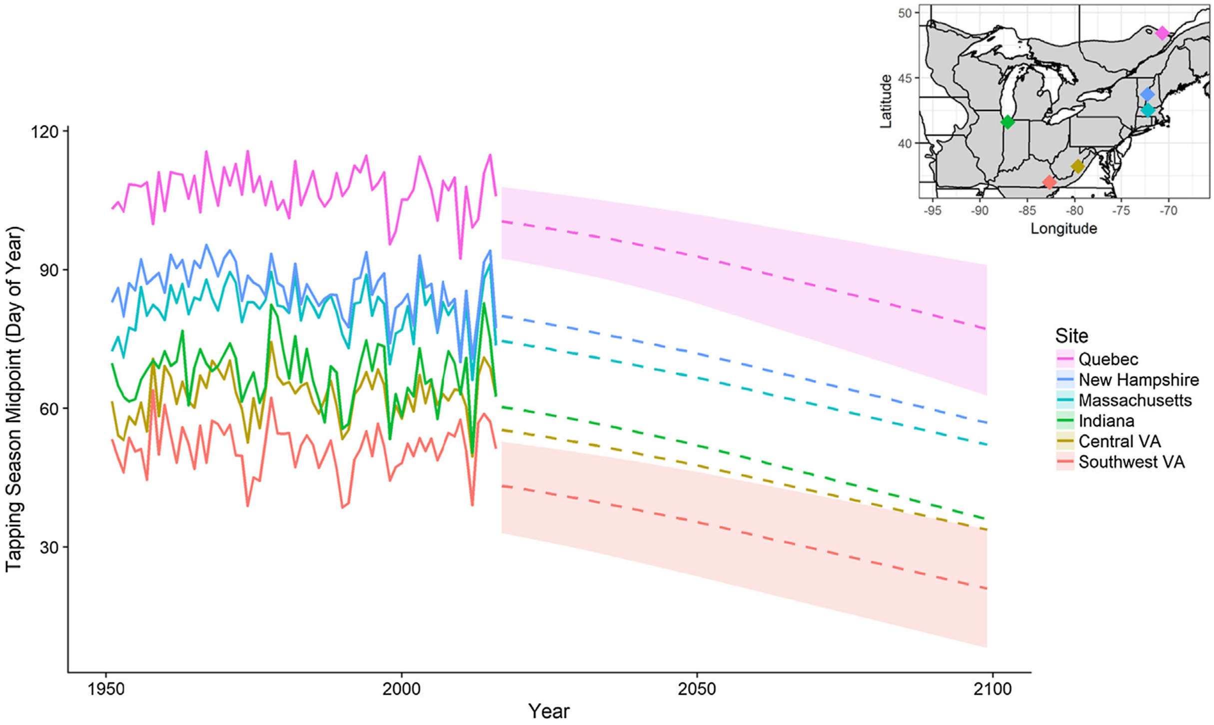

Fig. 4. Historical and future projections of the midpoint of sap collections based on mean tapping season (January – May) temperature. Projections from 1950 to 2016 are based on historical temperature data (solid lines), while projections from 2017 to 2099 are based on future climate projections from 14 statistically downscaled climate models. Dotted lines show a spline fitted through the projections of all 14 climate models, while the bands show the 95% prediction interval for selected sites. Gray shading on the insety map depicts sugar maple's distribution.

(1,64) = 4.904, $p = 0.0304$, $R^2 = 0.06$) declined over time.

With respect to our future projections, we found that projected tapping season midpoints showed a clear trend toward earlier timing by the end of the century for all sites, with the midpoint of the tapping season being about one month earlier by the end of the century compared to the historical period for all sites (Fig. 4; Table S5). Projected inter-annual variability and temporal trends in total sap collected depended strongly on location along the latitudinal climate gradient (Fig. 5; Table S5) and ranged from a decrease in collected sap to an increase in collected sap. Sites at both the warm and cold extremes of the climate gradient (Quebec and Virginia) had the lowest average and largest inter-annual variability in projected total sap collection in the historical period (Table S5). Our projections suggest that sap collection will be negligible in our warmest sites in Virginia and Indiana by the end of the century, while the most northern site in Quebec is projected to more than double. Our New Hampshire and Massachusetts sites were projected to have the smallest change in total sap collected, although are projected to decrease.

With respect to sap sugar concentration, future projections showed a clear trend toward lower and more variable sugar content by the end of the century (28–36% lower across sites; Fig. 5).

We found that inter-annual variability in projected total syrup production was greater for sites in the warm and cold extremes of sugar maple's range, rather than more moderate sites (Table S2). Projections indicated dramatic and mostly negative changes in syrup production per tap by the end of the century (Fig. 5). Sites in Virginia and Indiana were projected to produce almost no syrup by the end of the century, while sites in Massachusetts and New Hampshire were projected to produce half as much as in the historical period on average. Only at the site in Quebec site do projections support an increase in syrup production, with a doubling occurring by the end of the century on average.

Range wide, the midpoint of the sap collection season was modeled to fall on average in March or later across three-quarters of sugar maple's range in the historical period (Fig. 6a), with very few years seeing a midpoint date before this threshold (Fig. S5a). By the end of the century, however, the sap collection midpoint is projected to be in March or later only half of the time or less across the southern two-thirds of sugar maple's range (Fig. S5e). On average, the tapping season is projected to be about a month earlier across sugar maple's range (Fig. 6i).

Results from our model for the historical time period showed the area with greatest sap collected using gravity tapping methods (L/tap) ran through the central part of the sugar maple's range (Fig. 6b). However, under future conditions this area appears to shift north by the end of the century (Fig. 6f). Through southern Ontario and Quebec, as well as the mountainous parts of New England and New York, and around the northern Great Lakes, total sap collected is projected to be within 10–20 L/tap on average of historical period projected averages (Fig. 6j). In sugar maple's northern range in Ontario and Quebec, 20–30 L/tap more sap per year is projected to be collected on average (Fig. 6j), with more good years (> 40L/tap collected; Fig. S5j). The opposite is projected for the southern half of sugar maple's range; 30–40 L/tap less sap per year is projected to be collected on average under the RCP 8.5 scenario with fewer good years.

Model results using historical climate data indicate that sap sugar content has been greater than 2.0 °Brix on average across most of sugar maple's range (Fig. 6c), with years less than 2.2 °Brix only in the southern part of sugar maple's range (Fig. S5c). Under climate conditions in an RCP 8.5 scenario, however, our model consistently predicts lower sap sugar content. Sap sugar content is projected to be 0.55–0.65 °Brix lower on average (Fig. 6k), with most years below 2.2 °Brix over most of the sugar maple's range (Fig. S5k).

Our model indicated that optimal syrup production conditions in the historical period stretched from Wisconsin, across the Great Lakes, through New York and New England and southern Ontario and Quebec, like the area of optimal sap flow (Figs. 6d and S4d). This area of optimal production is projected to shift northward by the end of the century,

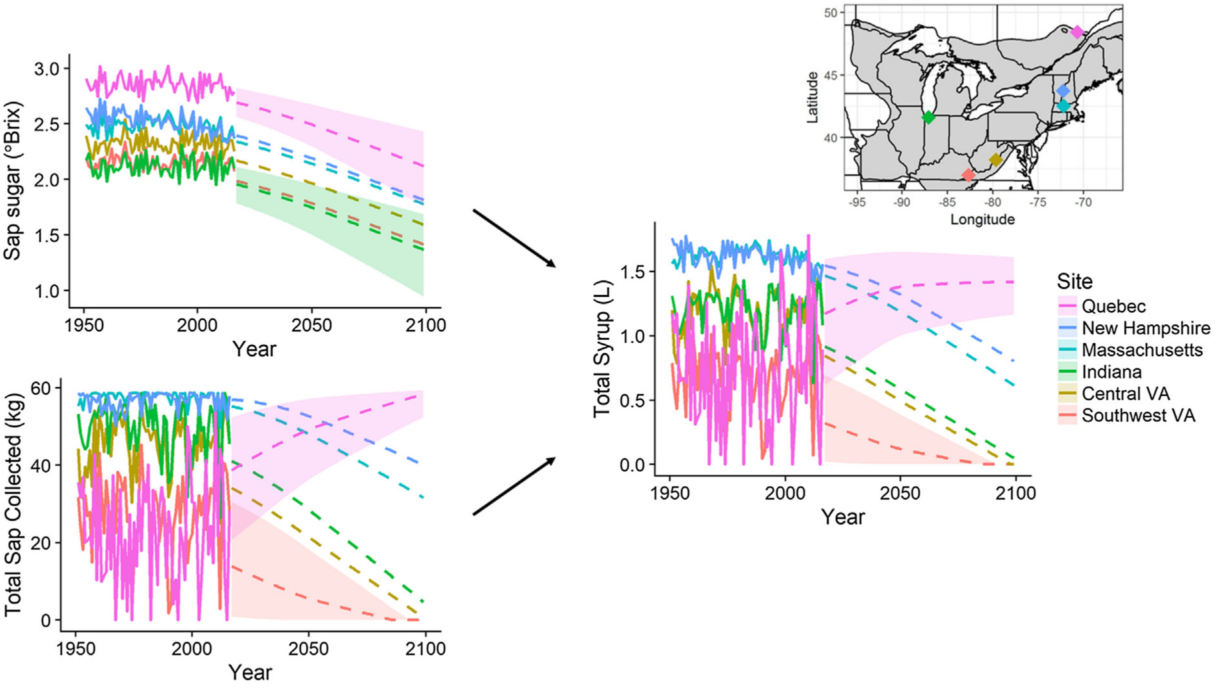

Fig. 5. Historical and future projections of total sap collected per tap based on mean tapping season (January – May) temperature, sap sugar content based on mean previous growing season (May – October) temperature, and total syrup produced per tap calculated from projections of total sap collected and sap sugar content. Projections from 1950 to 2016 are based on historical temperature data (solid lines), while projections from 2017 to 2099 are based on future climate projections from 14 statistically downscaled climate models. Dotted lines show a spline fitted through the projections of all 14 climate models, while the bands show the 95% prediction interval for selected sites.

with lower average production (Fig. 6h). Total syrup production is projected to decline over most of sugar maple's range by the end of the century, except for the far northern range in Ontario and Quebec which project to have moderate to large increases in average syrup produced per tap (Fig. 6l). Across the southern two-thirds of sugar maple's range, most years project to have production of less than 1L/tap of syrup (Fig. S5h), the traditional benchmark for production. Only along the northern range limit of sugar maple in Quebec will the number of years with production greater than 1 L/tap increase (Fig. S5l).

4. Discussion

4.1. Shifting climate optima for syrup production

Our results indicate a potential geographic shift in climate conditions for maple syrup production over the next century. We show that mean tapping season (January – May) temperature influenced the timing and number of freeze/thaw cycles and sap collection days, as well as the total amount of sap collected. In addition, sap sugar concentration was negatively related to the previous growing season (May – October) mean temperature, consistent with our expectation that climate conditions in the previous summer influence nonstructural carbohydrate storage, with higher temperatures leading to lower carbon stores. These relationships suggest a climatic optimum for maple syrup production that is currently centered around the Great Lakes, New England, and southern Quebec. This region currently accounts for the majority of global maple syrup production (National Agricultural Statistics Service, 2017, Statistics Canada, 2018), with maple syrup yield showing little variability across this region (Duchesne and Houle, 2014).

Our predictive model further indicates that climate change will drive changes in the optimal conditions for maple syrup production in two important ways. First, the tapping season is projected to be about a month earlier in most of sugar maple's range in North America, a result consistent with a number of studies (Duchesne et al., 2009; Guilbert et al., 2014; Skinner et al., 2010; Houle et al., 2015). Second, maple sap sugar content and the amount of maple sap collected (L/tap) under gravity tapping is projected to decline across much of sugar maple's range in the United States, leading to a decline in total syrup production per tap in most areas. However, maple sap volume is projected to moderately increase in northern Maine and along the northern range limit of sugar maple in Canada. As a result, climate impacts on maple syrup production is expected to be negative over most of the U.S. range of sugar maple and southern Ontario and Quebec but be near neutral or positive over the rest of the Canadian range of sugar, potentially driving a northward shift in production. Such changes may have profound implications for the maple syrup industry and for communities that culturally value sugar maple trees, especially in the United States.

Prior studies have used three approaches to project future changes in sap flow and/or syrup production, each of which have limitations that our study attempted to address by using a unique set of standardized empirical observations of sap flow and sugar content across the full production range of sugar maple, a latitudinal gradient across much of Eastern North America. One prior modeling approach projected sap flow based on modeled temperature data, estimating the timing and number of freeze/thaw cycles from projections of daily temperature ranges and using temperature thresholds for sap flow (Skinner et al., 2010; Guilbert et al., 2014). A limitation of this approach is that it does not consider sap sugar content, which our study and others (e.g. Pothier, 1995) provide evidence of being vulnerable to climate factors. Nor does this approach use *in situ* data on either sap flow or syrup production to constrain projections, which our approach does. A second approach focused on how climate may affect the availability of trees to tap (Matthews & Iverson, 2017), but did not consider trends or variability in sap or syrup production on a per tap basis. In the current study, we used a standardized sampling protocol over the entire range of sugar maple which allowed us to demonstrate geographic variation in the tapping season as it pertains to measurable climate parameters and thus to model shifts in the tapping season from the southern to the northern range limit of the species.

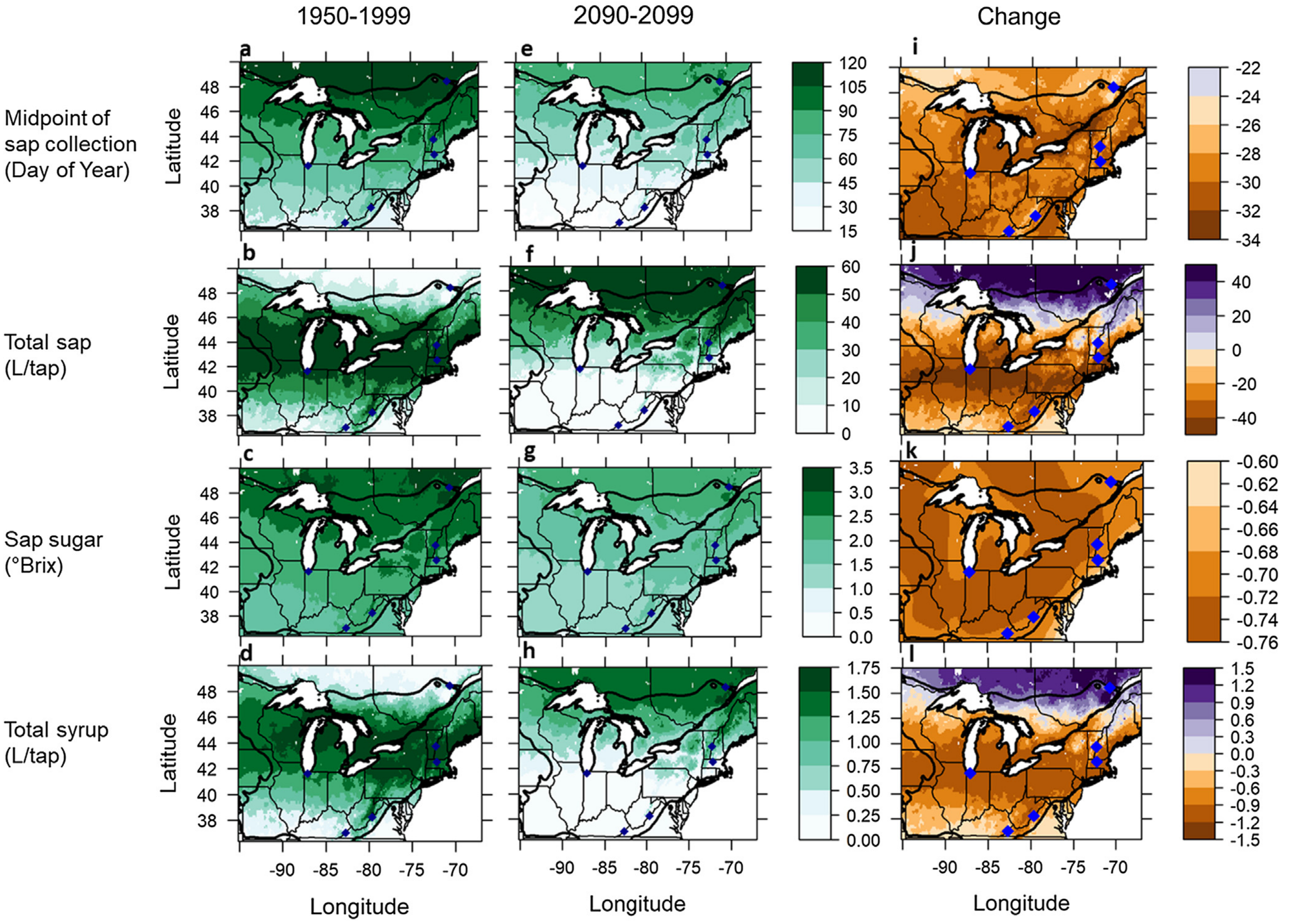

Fig. 6. Projections of mean values for sap metrics for the historical period (a–d) and the end of the century (e–h), and the change in mean value between the historical period and the end of the century (i–l). Blue diamonds show the locations of ACERnet sampling sites, while the thick black line shows the current range limit for sugar maple. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

A third approach to modeling climate impacts on maple syrup production, which derived empirical relationships between syrup production and climate, only used data aggregated over political regions that cover only a part of sugar maple's range (Duchesne et al., 2009; Houle et al., 2015). Since maple production is not distributed continuously across these areas, there is a potential mismatch between the climate and production data. In addition, rapid technological advances and expansion of tapping over the past decade (Farrell and Chabot, 2011; McConnell and Graham, 2016; National Agricultural Statistics Service, 2017) may confound the detection of climate-related temporal trends in these studies. Our current study removed this variability in production because of different methods of sap collection, and additionally allowed for the analysis of sap and climate data on a similar scale. Moreover, our methods included data on maple syrup production from the southern boundary of sugar maple's range. The climate of this region is expected to be indicative of future conditions in more northerly parts of sugar maple's range, giving special importance to understanding the current relationship between climate and maple syrup production in the region. We also projected that the greatest impacts of warming on maple syrup production are likely to occur in this region.

4.2. *Physiological mechanisms and potential effects of other site factors*

While most variation in sap collection timing was related to mean tapping season temperature, climate explained only 19–44% of the variation in the other metrics of syrup production, indicating that other factors affect parameters of syrup production. Sap flow volumes and sugar content are known to be influenced by tree characteristics and local site conditions (Morrow, 1955; Marvin et al., 1967; Blum and Koelling, 1968; Koelling, 1968; Smith and Gibbs, 1970; Blum, 1971; Gabriel et al., 1972; Plamondon and Bernier, 1980; Kim and Leech, 1985; Milburn and Zimmermann, 1986; Johnson and Tyree, 1992; Larochelle et al., 1998; Tryhorn and DeGaetano, 2011; Brown, 2013; Tamini et al., 2015; Caputo et al., 2016). Additionally, nonstructural carbohydrates provide the source of sugar in sap and may be influenced by masting patterns in sugar maple (Rapp and Crone, 2015). Soil freezing stress (Robitaille et al., 1995), stand nutrition (Wild and Yanai, 2015), and tree canopy size (Morrow, 1955) are also implicated in the sap sugar concentrations. While improved stand-level forecasts would likely benefit from incorporating these influences in models, our study shows that even with the variability inherent in stand-level sap collection, climate has a measurable effect that impacts maple syrup production range wide.

4.3. *Implications for management*

Findings from this study have the potential to inform maple syrup producers and policy makers who need evidence-based management plans to mitigate climate risk in the sugar maple industry. As maple producers are already reporting that the season for tapping sap from maple trees has changed in the past decade (Mozumder et al., 2015; Murphy et al., 2012), and that climate change is a concern for future syrup production (Legault et al., 2019) actionable science is acutely needed. A key insight from this research is that mean climate conditions are predictive of maple syrup production, at the site level. While previous research has reported links between climate and syrup production (Duchesne et al., 2009; Duchesne and Houle, 2014; Houle et al., 2015), these studies have used syrup production data aggregated at broad scales, and used more derived climate metrics such as accumulated growing degree days and the frequency of freeze/thaw events. While projections using these more refined climate measures may be more precise, mean climate conditions can be forecast more accurately on scales of a few months to decades. Sugar makers could therefore use long-term weather forecasts (2–3 months) to gain insight into the timing of the sap collection season, as well as whether sap harvests are likely to be large or small. Producers could also use summer temperature as a predictor of sap sugar concentrations in the following year. Likewise, forest managers and policy makers could use climate projections with confidence to make decisions that could impact future maple sap harvests.

Further research is needed to identify management practices to help syrup producers adapt to climate change. For example, demand for syrup and related products has led to the ubiquitous use of a wide variety of technologies meant to increase production, including vacuum tubing (Kelley and Staats, 1989) that mitigates freeze-thaw cycle controls on sap flow, and novel spouts to enhance sap collection (van den Berg et al., 2016). But whether and how these practices affect overall tree physiology (Wilmot et al., 2007; Isselhardt et al., 2016) and climate effects on sap quality and quantity require further study. In the Northeastern United States, large forested areas are being converted primarily for maple sap production, another practice that requires assessment. A variety of agroecological management strategies for climate adaptation have been proposed for other plant-based ecosystem services, ranging from species/varietal substitution, to technological changes and post-harvest practices, as well as migration and relocating production systems to more suitable locations (Ahmed and Stepp, 2016). Given the rapid increase in maple syrup production and its expanded role in local economies in many rural places of northeastern North America (Farrell, 2013; National Agricultural Statistics Service, 2017), our work highlights a spatial and temporal focus for these adaptation activities, and allows better planning for maple syrup producers, large and small. Sugar maple producers and resource managers can apply these results to design plans and policies to minimize climate risk. In addition, our findings are similarly relevant to indigenous communities of North America who have a long cultural history of tapping sugar maple trees before the arrival of Europeans (Keller, 1989; Turner and von Aderkas, 2012).

Declaration of Competing Interest

None.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.05.045.

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