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Sugar maple responses to climate change: We'll boil it down for you

ABSTRACT

In our recent article, we use *in situ* ecophysiological data from individual sugar maple trees across the species' range to identify climate conditions that maximize the volume and sugar concentration of sap. Houle and Duchesne present a critique of our research that hinges on their own analysis of industry aggregate data on syrup production, from within the latitudinal range where the industry is currently concentrated. Their approach falls short of both a proper validation of our ecological model and a rigorous comparison of two potentially complementary contributions. Notably, the aggregate dataset that Houle and Duchesne analyze includes an arbitrary mix of traditional gravity tapping and vacuum tubing extraction of sap, where the latter can maintain sap flow in the absence of freeze/thaw dynamics. In contrast, we hold the collection method constant, avoiding the confounding effects of vacuum tubing collection. Thus, their model conflates historical climate data with ongoing changes in sap extraction methods, and thereby masks relationships between climate and the volume and sugar concentration of sap. Moreover, by using regionally constrained aggregate data, Houle and Duchesne fail to capture the breadth of the species' responses to climate, which are represented in our dataset by populations at the edges of the species range. By ignoring these and other deep methodological discrepancies between their analysis and ours, Houle and Duchesne inappropriately put forth their own study as 'validation' of our ecological model. Unfortunately, this approach distracts from collaborative interdisciplinary discourse that could help refine predictions about sugar maple responses to climate. In our reply below, we refute Houle and Duchesne's unfounded *ad hominem* claims that our paper predicts a collapse of the maple syrup industry or is 'alarmist' in any way, and we clarify our contribution where they otherwise mischaracterize or misunderstand our work. We maintain that our model suggests a climate optimum for syrup production, based on range-wide data on the underlying ecophysiological responses of individual trees. We further point out where future research could address gaps in our knowledge of climate effects on tree physiology (the focus of our research) and on the syrup industry itself (which appears to be the aim of Houle and Duchesne's analysis here). We close by inviting researchers and syrup producers to join ACER-net, our collaborative science and outreach platform for understanding sugar maple and its ecosystem services in a changing world.

1. Introduction

In our recent article (Rapp et al., 2019), we project a latitudinal shift in the climate conditions that maximize the volume and sugar concentration of sugar maple (*Acer saccharum*) sap, based on *in situ* ecological data from individual trees across the species' range. Houle and Duchesne question our approach and present their own study, using aggregated industry data on syrup yield from producers within a narrower latitudinal range. We are very open to constructive dialogue about our work and would welcome a careful analytical comparison of these two studies, as the contrasting models, methods, and data can potentially advance our knowledge of the effects of climate change on maple sap. However, Houle and Duchesne fail in two principal ways to offer such constructive dialogue here. First, they misrepresent the core conclusions of our study and appear to misunderstand various details of our model. Second, they fail to identify crucial discrepancies between their analysis and ours, and so fall short of both a proper validation and a rigorous comparison of two potentially complementary contributions. In the interest of meaningful scientific discourse, here we clarify our contribution, identify a number of problems with their criticisms of our work, and identify key differences between our research and theirs. We close by summarizing how this discussion reveals potentially fruitful directions for future research on maple sap exudation and syrup production in a changing climate.

2. Misinterpretation of our conclusions

To begin, we categorically reject their suggestion that our article implies the "collapse of the U.S. maple syrup industry" as well as their value judgement that our conclusions are alarmist. Our findings, which are based upon ecophysiological data from individual trees across the species range, suggest a decline in sap volume and sugar concentration in some parts of the range, and an increase in others, over the next 50–100 years. These gradual ecophysiological changes could ultimately impact syrup production in negative or positive ways, depending upon climate conditions and geography. Houle and Duchesne's argument that we predict a market collapse of any kind is simply incorrect. On the contrary, our study is focused on the ecological responses of sugar maple trees to climate. We present a balanced view of our ecological results with a discussion that includes appropriate caveats about the limitations of the model. We clearly explain in our discussion that a number of other environmental variables could influence the quality and quantity of sap. We also point out that changes in tapping methods could offset climate-driven responses of individual trees. As we state in our article, more research is certainly needed on the physiological changes of trees as well as the adaptive responses of syrup producers to offset those changes. However, whether or not our findings have negative implications for economic investments in the industry is beside the point, would likely be affected by a host of socioeconomic influences beyond the scope of this study, and certainly should not guide whether or not we report the results.

Further, the characterization of our work as alarmist is curious in light of our critics' own previous research (Duschene and Houle, 2014) reporting that climate change may indeed favor maple syrup production in the north. That Houle and Duchesne are so preoccupied with representing our results as alarmist and fail to note that they have independently reached conclusions similar to ours in a previous study (which we cite in our article) impedes a genuine productive discourse

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about our research.

3. Inappropriate model validation

A second major flaw in Houle and Duchesne's critique involves their follow-up modeling exercise that attempts to refute our general conclusions and again directly conflicts with their own prior work. They base their model on *regionally constrained industry aggregate data from syrup producers* that are incongruent with our *ecological data on sap production by individual trees from across the species' range*; as a result, it is not particularly telling that their conclusions are different from ours. Notably, their data include reports by producers using both traditional tapping and vacuum tubing methods of sap extraction, where the latter can maintain sap flow in the absence of temperature forcing (freeze/thaw dynamics). As our article specified, the underlying sap data we used to train our model came from standardized collection from gravity-tapped individual trees, as we were primarily concerned with ecological responses of sugar maple to climate change. We thus observed individual trees in conditions of natural atmospheric pressure while holding the collection method constant for analytical rigor. In our article, we describe how vacuum tubing methods are a growing practice in the maple syrup industry that may help producers adapt to the effects of climate change. By incorporating vacuum tubing collection in their data, Houle and Duchesne conflate historical climate data with ongoing changes in sap extraction methods, and thereby mask relationships between climate and the volume and sugar concentration of sap.

The scientific community can certainly benefit from more research on differences between vacuum tubing and gravity-tapping methods in an effort to help syrup production remain stable despite climate change, and perhaps Houle and Duchesne's new analysis can contribute to that endeavor. However, the methodological discrepancies between their analysis and ours make it inappropriate to interpret their study as a 'validation' of our ecological model. Further, using regionally constrained aggregate data that include an arbitrary mix of different tapping methods, they cannot speak to our conclusion that there is a climate optimum for the volume and sugar content of sap produced by individual sugar maple trees.

4. Site location and representativeness across the geographic range

On a related note, we challenge Houle and Duchesne's objection to our use of sites near the limits of sugar maple's range. They argue that our study should have focused on the geographic area where the maple syrup industry is concentrated (as they did in their modeling exercise described above) rather than on the full range of sugar maple. We disagree. Constraining the study to a narrow latitudinal range runs counter to general precepts in ecological modeling. Trailing edge populations usually occupy the climatic extremes and thus can be an early indicator for species' responses to climate change. The research design for a study of climate effects on maple sap volume and sugar concentration should therefore not be influenced by any aspect of the maple syrup industry, but rather, by the potential range of climate conditions that could affect tree physiology. Furthermore, the authors assert that the Massachusetts site alone explains the projection of a climate optimum, but this is precisely the point; Massachusetts represents an approximate mid-point in the temperature range of the study, and the results show that sap quality and quantity are lower north or south of that region. As we note in our article, we included site and year as random effects in our model to compensate for variation related to possible underlying site features (e.g., prior year climate conditions, soil type or nutrient status) that might also affect sap volume and sugar concentration. Thus, we maintain that our sampling design is sound: while acknowledging potential contributions of site-specific factors, we make projections about future sap volume and sugar concentration with ecophysiological data representing the climatic range of the species.

Additional sites across the species' range would be highly informative regarding site-specific characteristics that could influence the model, as we acknowledge in our article. Since collecting sap from individual trees in a standardized manner across multiple sites is a time-consuming and laborious endeavor, we would welcome future collaborations that add data on sap volume and sugar concentration from more sites across North America. We encourage interested producers and scientists to consider joining ACERnet (https://blogs.umass.edu/acernet/), a network we formed to promote collaborative science and community needs assessment on this issue.

5. Model details

That Houle and Duchesne mischaracterize our findings and use an incongruent dataset to 'validate' our results largely impedes a productive dialogue about our research. Their remaining critiques indicate some misunderstandings about our work or simply point out the limitations of any ecological study or modeling endeavor. To clarify for readers, we address these minor points below.

5.1. Temperature and sap sugar content

Their assertion that we "speculate that high temperatures during the previous summer lead to a negative carbon storage budget …" is a mischaracterization of our interpretation of the negative relationship between sap sugar content and the previous growing season temperature. The correct interpretation is that as temperature increases, the difference between the amount of carbon fixed by photosynthesis and the amount released by respiration becomes smaller, with less carbon available to be allocated to storage as nonstructural carbohydrates, which in turn is the source of sugar in sap. A negative relationship does not imply that respiration releases more carbon than photosynthesis fixes (i.e. a negative carbon budget). As we were testing a specific hypothesis, we did not test the effect of additional climate variables on sap sugar content. Our specific hypothesis that sap sugar content was inversely related to previous summer temperature is supported by Figure 3c, not only when the data are pooled across all sites but also with regard to the means for each site in most cases. For all but one of the sample sites, mean sap sugar concentration had a negative relationship with previous growing season mean temperature. It is a mischaracterization to state, as Houle and Duchesne do, that the relationship is driven solely by the spatial gradient.

We further note that the previous studies cited by Houle and Duchesne (Duchesne et al., 2009; Duchesne and Houle, 2014; Rock and Spencer, 2001; Tyminski, 2011) did not test the effect of winter temperatures on *sap sugar*, as we did, but on *syrup yield*. Duchesne and Houle (2014) also reported a positive relationship between maple syrup yield and previous year growing degree days in a multiple regression model with several other predictors. They interpreted this relationship as support for the hypothesis that warmer growing seasons result in greater sap sugar content, but they measured syrup production (again possibly including data from producers using vacuum tubing), not sap sugar content. While our study directly tests the effect of previous growing season temperatures on sap sugar content, in the prior studies cited above it is unclear whether winter temperatures affect sap sugar, sap volume, or both. Thus, we contribute unique data to disentangle the effects of climate on sap volume and sugar concentration. The fact that prior findings on climate and *syrup yield* are mixed with regard to agreement with our findings for *sap sugar concentration* of course suggests the need for more interdisciplinary research.

5.2. Indicator variables for sap yield and suggestion to build regional models

Houle and Duchesne question the use of average five-month temperature (January to May) as a predictor of sap yield for a given year. They suggest creating regional models – using a different tapping season month for each site and/or predicting sap yield based on the number of nights below freezing. We disagree that creating region-specific models based on number of freeze/thaw cycles would be a better approach for this study. First, the power of a range-wide sugar maple sampling design is that we can test a wider range of climate conditions than year-to-year variability at single sites would allow. We recognize that site-to-site variability is important to consider with a range-wide model but, as we already mentioned, we included site and year as random effects in the model to account for this. Fitting only site-specific models would negate this power and allow projections only at specific sites and not range-wide. Second, with a range-wide model it is important to use the same predictor across all sites based on which independent variable has the most predictive power. As we describe in our methods, we fitted models with a variety of alternate independent variables, including all mean monthly temperatures from January through May, as well as the number freeze/thaw cycles and the seasonal average temperature. We selected the latter because it was the best predictor of sap yield.

5.3. Accounting for variability and presentation of results

Regarding the modeled fit in Figure 3b and the intercept reported in Table 2, we refer back to the methods section of our article. As we state on page 190, we include site and year as random effects in the model to account for interannual and site-level environmental variation (e.g., soil type, nutrient conditions, prior year temperatures, and other unmeasured variables). The intercept generated by that model appears in Table 2 and captures the site-level variability in climate-sap relationships. For the figure, we show a single line of best fit, which is more broadly applicable across a range of climates. This figure was generated using the “predict.merMod” function in R with re.form = NA, which fits the model without random effects. An alternative would be to show a separate line for each study site in each year, but since our objective is to make predictions across the range we collapse the data into a single predictive curve. The R code for the alternative figure is available upon request. Regarding Figure 5, Houle and Duchesne are correct that the variability in the model comes from the variability in climate projections. As discussed above, this is appropriate. Our model is concerned with the effects of climate on sap volume and sugar concentration across the range, rather than site by site or region-specific predictions.

6. Closing thoughts

In summary, we maintain that we found evidence for a climate optimum for syrup production based upon a standardized protocol for sap collection from individual trees under natural conditions. By modeling relationships between climate, sap flow, and sugar concentration we contribute to understanding the basic ecophysiological responses underlying climate effects on syrup production. Houle and Duchesne hinge their dismissal of our work on *ad hominem* claims that our paper is alarmist, and on their analysis of a separate data set that is inappropriate for validating our empirical model. This approach unfortunately distracts from the collaborative interdisciplinary research that is needed to deepen our understanding and to refine predictions about sugar maple responses to climate.

We would like to suggest some key knowledge gaps for further investigation: 1) to what extent vacuum forcing of sap can offset declines in syrup production that result from direct effects of climate on tree physiology; 2) whether there are geographic differences in the physiological responses of maple trees to climate; and 3) how interannual and geographic variation interact with climate to influence sap volume and sugar concentration. Additional lines of inquiry could include a better understanding of carbon budgets in maple trees, especially the particularities of winter and prior year temperatures on sap sugar, sap volume, or both.

How our predictions are supported remains to be seen, but we remind readers that our projections are on the scale of a half-century or more. Meanwhile, we are expanding upon our ecological studies with social science data, to gain a broader understanding of how maple tappers and other stakeholders perceive climate effects on sap collection and other social and economic phenomena surrounding sugar maple and its ecosystem services. We also continue to seek opportunities to collect ecological data from more locations, to add to the predictive power of our model and assess the contributions of site-level characteristics to sap quality and quantity. To that end, we invite other researchers and producers across the range of maple to join ACER-net, such that we can continue to ask important questions regarding maple sap exudation and climate change.

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Joshua M. Rapp[a,b], David A. Lutz[c], Ryan D. Huish[d], Boris Dufour[e], Selena Ahmed[f], Toni Lyn Morelli[g], Kristina A. Stinson[a,*]
[a] *Department of Environmental Conservation, University of Massachusetts Amherst, 160 Holdsworth Way, Amherst, MA 01003, USA*
[b] *Harvard Forest, Harvard University, 324 N. Main St., Petersham, MA 01366, USA*
[c] *Environmental Studies Program, Dartmouth College, 6182 Steele Hall, Hanover, NH 03755, USA*
[d] *Department of Natural Sciences, University of Virginia's College at Wise, 1 College Avenue, Wise, VA 24293, USA*
[e] *Université du Québec à Chicoutimi, Département des Sciences Fondamentales, 555 Boul. de l'Université, Chicoutimi (Québec) G7H 2B1, Canada*
[f] *Department of Health and Human Development, Montana State University, Bozeman, MT 59717, USA*
[g] *Northeast Climate Adaptation Science Center, U.S. Geological Survey, Amherst, MA 01003, USA*
E-mail address: kstinson@umass.edu (K.A. Stinson).

* Corresponding author.