

Ranger Outline: We will come up with a better title
when we feel more grounded in the results

Dan, Cat, Nacho and Lizzie and the lab

Abstract

Introduction

For woody plants of the temperate zone the phenology, or annual timing, of spring budburst influences a myriad of ecological processes including patterns of resource allocation (), trophic interactions () and biogeochemical cycling (). Through budburst timing, woody plants balance the advantages of precocious growth resumption for resource gains with the risk of damage from late season frost (). To navigate this tradeoff, woody plants have evolved complicated networks of sensory organs, hormone signaling, and physiological responses to sense environmental cues; changes in their physical environment, that signal the arrival of appropriate conditions for resuming growth.

Decades of research suggest that warming spring temperatures (forcing), cool winter temperatures (chilling) and day length (photoperiod) are primary environmental cues utilized by woody plants that determine the timing of spring phenological events . These studies also demonstrate the there are substantial cue-use differences among species, with some species relying more heavily on some cues over others (Laube et al., 2014). As anthropogenic climate change has already driven shifts in spring phenology (), identifying these interspecific differences in cue use has emerged as a major goal of phenological research (). These differences have strong implications for both predicting the rate of phenological shifts as the climate continues to warm (), and anticipating the ecological consequences of these shifts ().

But the quantification of cue use difference among species offers even more—a novel opportunity to interrogate long-standing theories regarding the biology underlying cue-use difference among species. One particular relationship that can now be examined is the relationship between species’ geographic ranges and phenological cue use.

Climate is the major selective force on both species’ geographic ranges (1) and their phenology (2), and therefore, it is widely assumed that phenological cue-use differences among species reflect correlation with the climate of their respective ranges (3). That is, a species’ relative reliance on forcing, chilling and photoperiod for each species should be shaped by the unique environmental conditions across a species’ geographic range.

This has never really been tested (say better but see (Zohner et al., 2017)). With the recent quantification for cue use of many species (4) and the accessibility of high resolution climate data it is now possible to rigorously test this theory with data. Below, we briefly review the specific assumptions and predictions presented in the literature about the relationship between phenological cue-use and species’ range characteristics. We then test these predictions using Bayesian models for a large suite of temperate woody species from North America and Europe.

Assumptions and predictions for the relationship between the cue-use and species’ ranges

Current understanding of the evolution of phenological cues assume that forcing is the predominant cue. In this framework, a secondary reliance on photoperiod and/or chill cues evolve when forcing alone is not a reliable cue of safe growing condition (Körner and Basler, 2010). Forcing is an unreliable cue when patterns of forcing are unstable in the spring time. In other words when forcing is variable. When considered at the macro-ecological scale, this conceptual framework predicts species with high variation in forcing in their range should have a stronger response to chilling and or photoperiod and a weaker sensitivity to forcing (Wang et al., 2014; Muffler et al., 2016). Here after, we refer to this as the range-cue use hypothesis

An implicit assumption the range-cue use hypothesis is that among species cue variation is higher than within species (ie cue use is “conserved” at the species level). If rather, cue use patterns are locally adapted, the range-cue use hypothesis would not hold. There is not yet a

strong consensus about to what degree cue use is locally adapted and it likely varies between phenophases (), and organisms (). As such, any analysis considering species ranges and cue use must account for intra-specific differences as well.

A major hurdle for testing the range cue-use hypothesis is that, when considered in the context of a species' geographic range, forcing variation occurs on multiple temporal and spatial scale.

1. Intra-annual variation (Temp.var ggdlf)
2. Inter-annual (cite Zohner) (Temp.var stv)
3. local climate variation (Geo.var ggdlf)
4. Deeper time stability () (literature)
5. global climate variation (continents). In general NA is more variable than Europe

Any of these level of variation could itself drive selection for secondary cue usage (photoperiod/chilling) and it is unclear how they interact or which is most important (Zagmajster et al., 2014). Understanding the relationships between spring forcing variation at multiple spatio-temporal scales is a second key to robustly testing the range-cue use hypothesis.

Predictions

For these theoretical frameworks we can make several predictions regarding the range-cue use hypothesis:

1. More STV or variation in GGD2lf should increase chill and photo sensitivity. Decrease forcing sensitivity. (First principles)
2. North America should increase chill and photo sensitivity. Decrease forcing sensitivity.

We tested these underlying assumptions about the relationship between climate variables in a species ranges and specific predictions for the relationship between range climate and cue use using the OSPREE database, and climate data, and models. Our interrogation of these relationships between climate and cue use not only clarifies the evolutionary drivers of cue use, but offers new insights regarding implications of climate change as both species' ranges and phenology continue to shift with warming.

Methods

Phenological data and cue-use estimates

Dan and/or Lizzie write:

- Introduce OSPREE
- Species selection
- Model description

Species' range characteristics

Cat and/or Nacho write?

- Climate data (**Figure of range maps with one climate variable, other could go to supplement**)
- note on temp vs. geographic variation
- calculation of GDD last frost
- STV

Secondary cue use

Dan write description of joint model

Statistical analysis

Intra vs. interspecific models

Cat

Results

Some combo of simulations and real data to talk about the coherence of gdd2lf, stv and geographic variability, and maybe a figure too. Model plots and ??fig:mods and 3 (not sure why my referencing isn't working) to show it is all futile and nothing matters.

Discussion

Things to address in the discussion:

1. Why differences between NA and EU show up for correlation between temp and geo variation, and STV and range area. (perhaps this is where we can talk about the artifact of STV not capturing “biological spring” across a large range)
2. In general why these continents show different trends
3. Alternative explanations: A ton of hypotheses about community dynamics, phylogeny etc

References

- Körner, C., and D. Basler. 2010. Phenology under global warming. *Science* 327:1461.
- Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014. Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology* 20:170–182.
- Muffler, L., C. Beierkuhnlein, G. Aas, A. Jentsch, A. H. Schweiger, C. Zohner, and J. Kreyling. 2016. Distribution ranges and spring phenology explain late frost sensitivity in 170 woody plants from the Northern Hemisphere. *GLOBAL ECOLOGY AND BIOGEOGRAPHY* 25:1061–1071.
- Wang, T., C. Ottlé, S. Peng, I. A. Janssens, X. Lin, B. Poulter, C. Yue, and P. Ciais. 2014. The influence of local spring temperature variance on temperature sensitivity of spring phenology. *Global Change Biology* 20:1473–1480.

Zagmajster, M., D. Eme, C. Fišer, D. Galassi, P. Marmonier, F. Stoch, J. F. Cornu, and F. Malard. 2014. Geographic variation in range size and beta diversity of groundwater crustaceans: Insights from habitats with low thermal seasonality. *Global Ecology and Biogeography* .

Zohner, C. M., B. M. Benito, J. D. Fridley, J.-C. Svenning, and S. S. Renner. 2017. Spring predictability explains different leaf-out strategies in the woody florals of north america, europe and east asia. *Ecology Letters* 20:452–460.

Figures

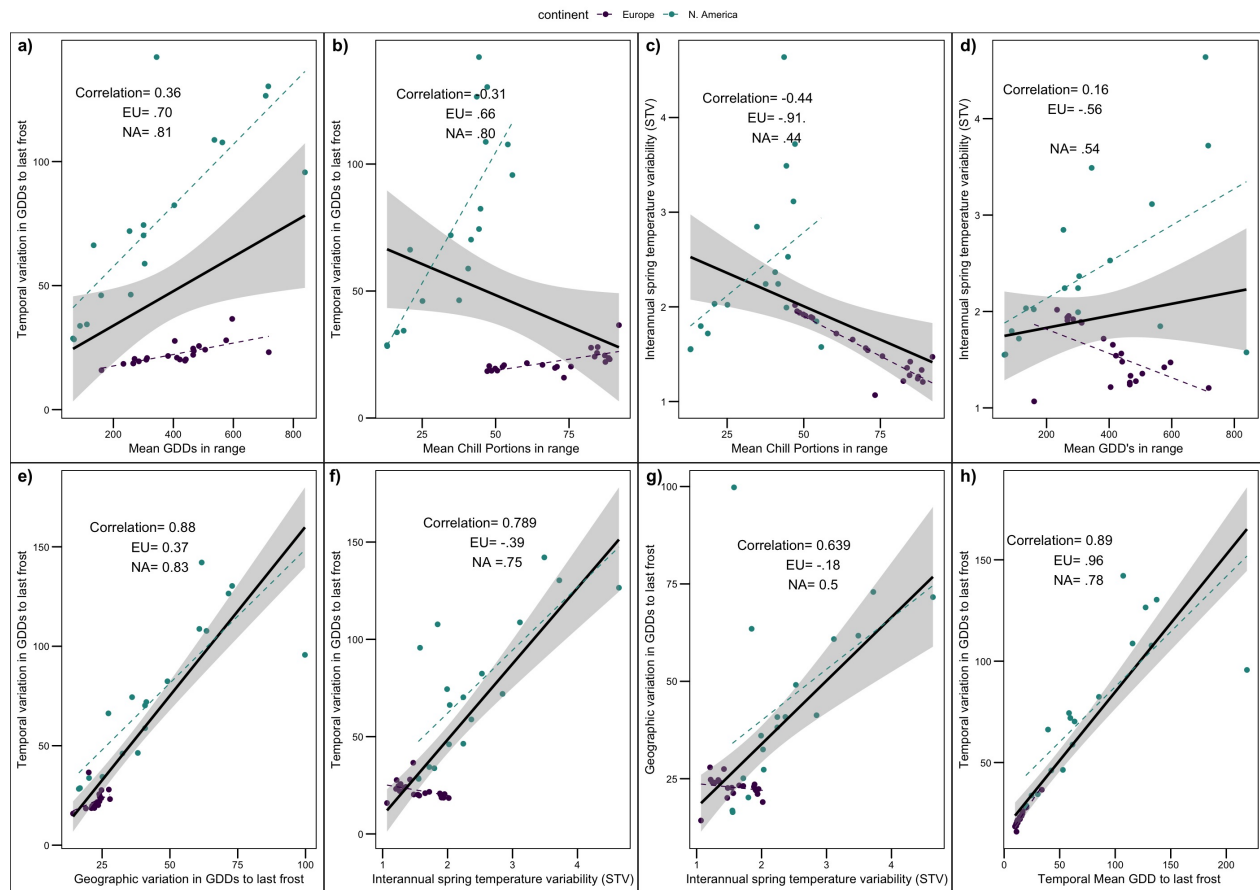


Figure 1:

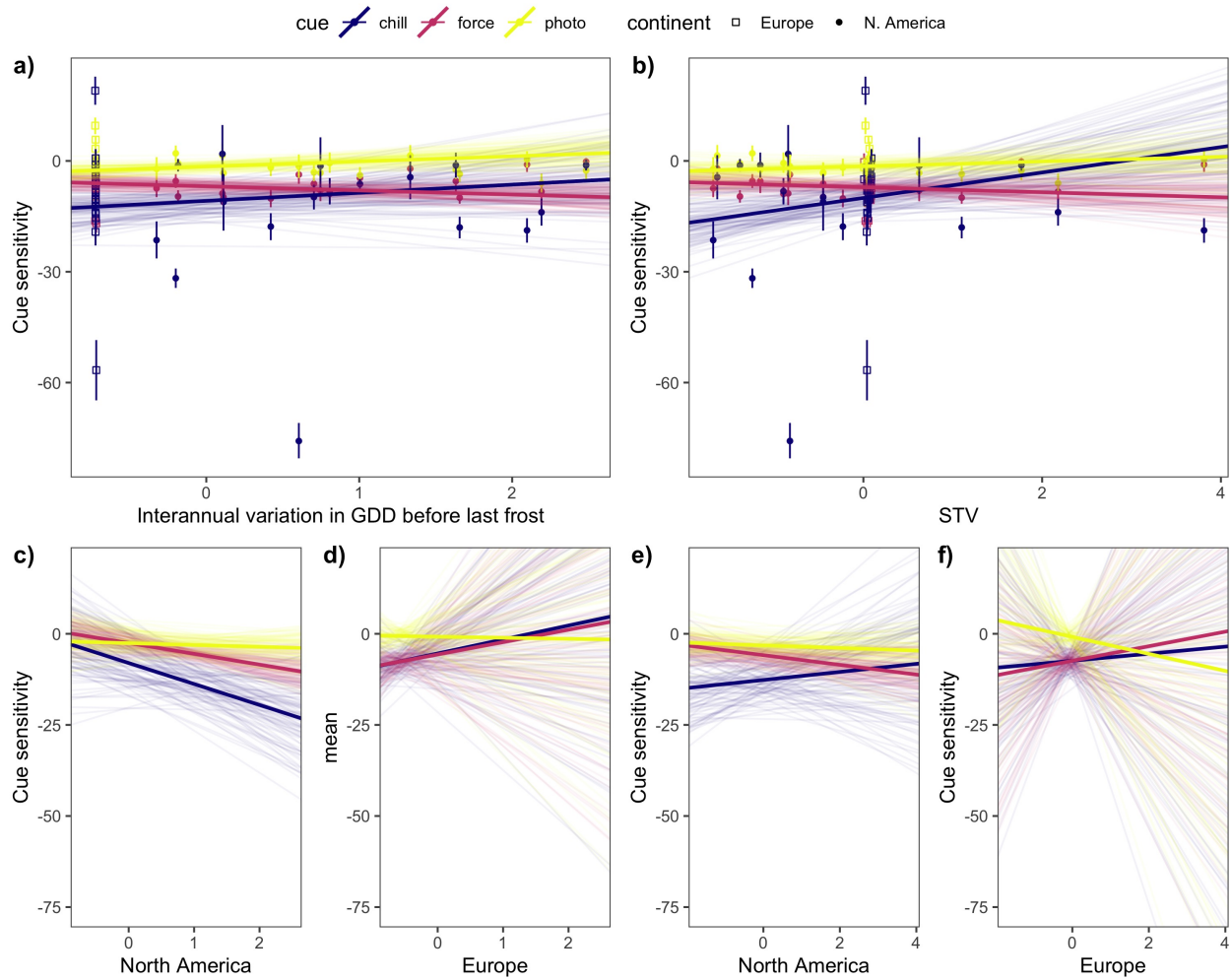


Figure 2: Who okay this figure is definitely under construction. Orange is gdd to last frost variation and green is stv. solid lines (on right pannels) North America and dashed is Europe. Is there a good way to demonstrate that the slopes fit the data poorly?

Tables

climate	Forcing	10%	90%	Photo	10%	90%	Chill	10%	90%
Mean Chill Portions	1.43	-1.70	4.53	0.53	-2.61	3.74	3.10	-0.17	6.44
Mean GDDs	0.11	-0.96	1.24	1.32	0.16	2.47	3.28	0.27	6.25
STV	-0.68	-1.90	0.55	0.66	-0.51	1.84	3.41	0.18	6.74
Var. GGD to last frost	-1.18	-2.58	0.22	1.41	0.01	2.81	2.40	-1.24	5.99

Table 1:

continent	climate	Forcing	10%	90%	Photo	10%	90%	Chill	10%	90%
Eu	Mean Chill Portions	1.84	-1.45	5.09	0.20	-3.03	3.43	1.85	-1.53	5.24
Eu	Mean GDDs	3.24	-5.47	11.63	-0.50	-9.13	8.19	4.05	-6.78	14.92
Eu	STV	1.47	-11.11	14.13	-2.22	-14.61	10.58	0.92	-11.64	13.61
Eu	Var. GGD to last frost	3.67	-7.73	14.81	0.11	-10.95	10.87	3.30	-7.94	14.36
N.A	Mean Chill Portions	0.69	-2.55	3.92	0.46	-2.78	3.58	3.90	0.24	7.53
N.A	Mean GDDs	-1.48	-2.43	-0.52	-0.31	-1.58	0.88	-3.65	-6.92	-0.31
N.A	STV	-1.29	-2.57	-0.05	-0.38	-1.99	1.18	1.12	-2.71	4.94
N.A	Var. GGD to last frost	-3.07	-4.97	-1.09	-0.46	-2.90	1.99	-5.94	-11.55	-0.24

Table 2:

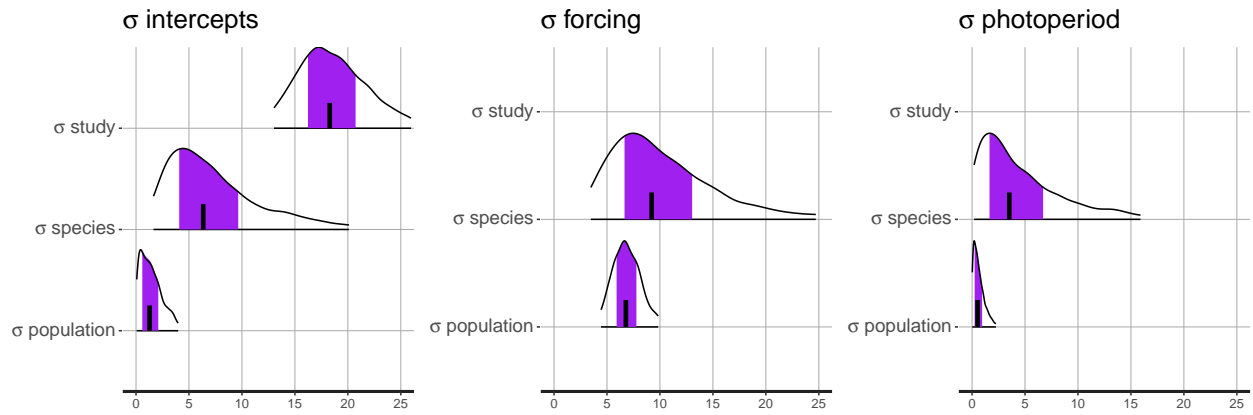


Figure 3: Interspecific variation exceeds intraspecific. Maybe Cat should write this?

	mean	10%	25%	75%	90%	continent
muChillSp	-5.66	-12.59	-9.28	-2.05	1.28	Eu
muPhotoSp	-0.52	-7.10	-3.88	2.95	5.84	Eu
muForceSp	-5.48	-12.42	-8.86	-1.99	1.36	Eu
muChillSp1	-7.91	-15.30	-11.74	-4.05	-0.59	N.A
muPhotoSp1	-2.59	-5.75	-4.21	-0.96	0.57	N.A
muForceSp1	-2.43	-4.91	-3.65	-1.16	-0.04	N.A

Table 3: