

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

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## Figures to make:

1. Climate maps for species (some in supp. too)
2. Conceptual figure illustrating why variation in forcing should impact cue use
3. Results from cheapo models
4. some comparison of North America to Europe
5. Results from inter vs. intra specific model

## 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 () and their phenology (), and therefore, it is widely assumed that phenological cue-use differences among species reflect correlation with the climate of their respective ranges (). 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 () 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. Here after, we refer to this as the range-cue use hypothesis

An implicit assumption of 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.

A possible alternative method that avoids this issue is to consider the relationship between range sizes and cue use. Rapoport's rule, a long established concept in biogeography suggest that species ranges should be larger closer to the poles (). The proposed mechanism underlying this pattern is increased climatic heterogeneity selects for larger range sizes (). While Rapoport's rule does not explicitly address climate heterogeneity in the early spring (the time relevant to leaf phenology), its general logic has been evoked to explain cue use patterns () and been broadly observed for temperate trees of North America (). However, it is unclear how generalizable Rapoport's rule is (Gaston and Chown, 1999) and its relevance to spring phenological cues should be tested explicitly.

## 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.
3. Larger ranges should correlate with increase chill and photo sensitivity. Decrease forcing sensitivity. (Rapoport)
4. More northern ranges should correlate with increase chill and photo sensitivity. Decrease forcing sensitivity. (Rapoport)

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
- range area

### Statistical analysis

#### Intra vs. interspecific models

Cat or Lizzie or Dan write

#### Range-climate correlations

Correlation coefficients for NA and EU (basically how we made fig 1 )

#### Secondary cue use

Dan write description of “Sequential modeling”.

Dan write about continent comparisons.

## Results

### Intra vs. interspecific

We found that inter-specific variation in cue use was higher than intraspecific.

### Coherence of forcing variation

1. Good correlation between spatial and temporal intra-annual variability (Fig 1 a)
2. Decent correlation between inter and intra-annual variability in North America but not in Europe (Fig 1 b,c)
3. Also please note the magnitude of variation between NA and Europe is quite different.

### Rapoports Rule in spring climate variability

1. Basic prediction (increase latitude correlated with larger ranges) of Rapoport's Rule is met for our species subset (Fig 1 d,e)
2. Predictions about range size and variability of climate variable not well supported (Fig 1 f-j though okay for STV in Europe panel h,i)

### Climate variation and secondary cue use

- mu plot for STV, ggglftemp and ggdlfgeo.
- Area by cue. centroid by cue.
- Discuss differences between NA and EU in above plots and that overall, North America does have stronger secondary cue use (Fig 2)

## 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. Not surprised we don't see Rapoport's rule strongly. It's not so well supported in general (Gaston et al., 1998)
4. Alternative explanations: A ton of hypotheses about community dynamics, phylogeny etc

## References

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- 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 floras of north america, europe and east asia. *Ecology Letters* 20:452–460.

## Figures

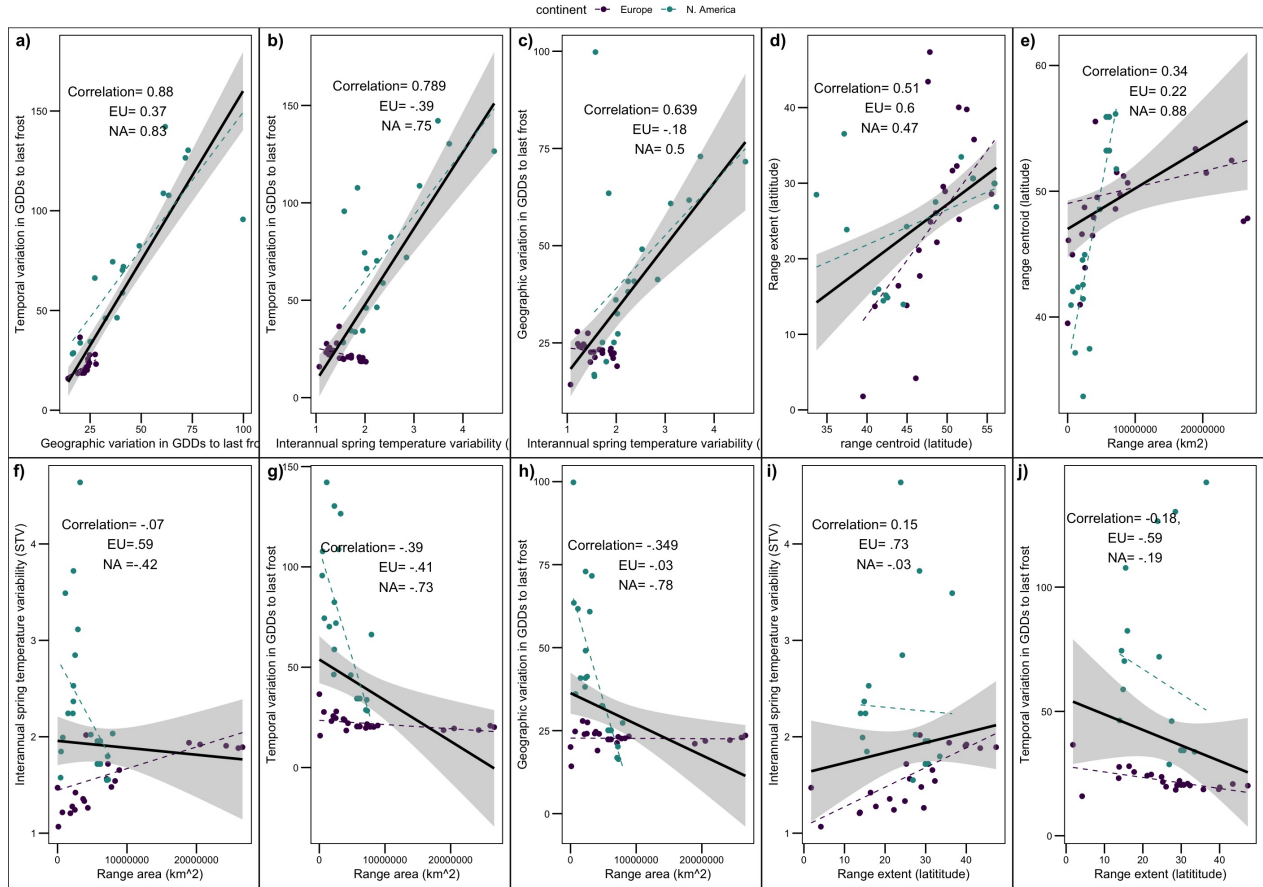


Figure 1: Correlations between levels of forcing variation.

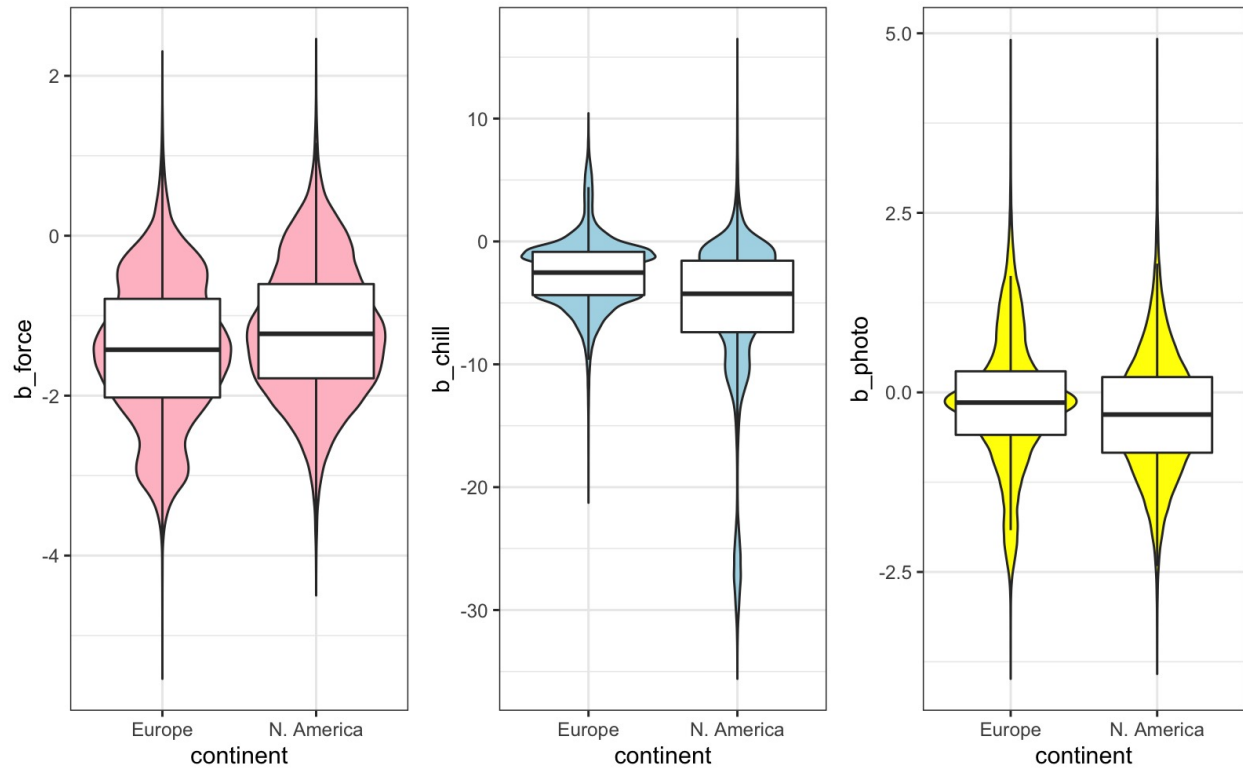


Figure 2: North American species which experience high spring forcing variation have stronger (more negative) chilling and photoperiod sensitivity and weaker (less negative) forcing sensitivity than European species. This is based on posertior estimates for each species grouped by continent