Continental divides: How the climate shapes the phenological cue strength of woody species in temperate North America and Europe

or

Spring climate stability shapes phenological cue sensitivities of temperate forest in North America but not Europe

or

Limited support for range-wide climate patterns shaping phenological cue differences among woody plants of temperate North America and Europe

or

Other

Dan, Cat, Nacho and Lizzie and the lab

November 5, 2021

1

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 this the relationship 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 correlate 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 outline two hypotheses presented in the literature about the relationship between phenological cue-use and species' climatic range characteristics. We then test these predictions using Bayesian models for a large suite of temperate woody species from North America and Europe.

0.1 Climate intensity hypothesis

One hypothesis for the evolution of cue use differences across species is that species utilize the climate cues to which they have the most exposure. Simply stated, there should be a positive correlation between the amount or intensity of a cue across a species' range and the species phenological sensitivity to that cue. This hypothesis predicts that species with a) high numbers growing degree days in their range should have stronger forcing cues, b) higher amount of chilling should have stronger chilling cues and c) more annual photoperiod variation should have stronger photoperiod cues. This hypothesis has been applied to explain large, macro-ecological patterns in phenology like why the tropical phenology cues primary to forcing and temperate and arctic phenology is more dependent on photoperiod and/or chilling () but has not been widely tested within biomes for species with overlapping ranges.

0.2 Climate variability hypothesis

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 is an unreliable cue when temperatures unstable in the spring time. The climate variability hypothesis predicts species with high variation in spring temperature in there range should evolve a stronger response to all three cues, especially chilling and or photoperiod, (Wang et al., 2014; Muffler et al., 2016). This hypothesis potentially explains the stronger cue sensitivity of temperate North American species to those in Europe where there is less climate variability in the spring (**?**).

However, a major hurdle to robustly testing this hypothesis is that, when considered in the context of a species' geographic range, spring temperature variation occurs on multiple temporal and spatial scale. Phenology may be shaped by intra-annual temperature variation (e.g.

frequency of late season frost, diurnal temperature functions), inter-annual variation (e.g. annual mean temperatures) and the interaction between them (e.g. inter-annual variation in last season frost episodes). Further, each of the level of variation be quite different across a species range, suggesting geographic variation with the range must also be accounted for. 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). Key to testing the climate variability hypotheses is to first characterize relationships between spring temperature variation at multiple spatio-temporal scales.

0.3 Local climate hypothesis

An implicit assumption of the previously stated hypotheses is that among species cue-use variation is higher than within species (ie cue use is "conserved" at the species level). If rather, cue use patterns are locally adapted, while climate intensity and climate variability may still drive cue-use patterns at the population level, it would be difficult to detect consistent patterns across a species full geographic range. 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.

0.4 Non-climate drivers of cue use

It is also important to recognize that though climate is the mechanism underlying woody plant phenology, there may be other selective forces driving cue use. Cue use differences may be the product of other tradeoffs. Could say this here or leave for the discussion.

We leveraged over 50 years worth of phenology experiments in the OSPREE database () and climate data collected across the ranges of temperate woody species to test the three major climate-cue use hypotheses. We used a Bayesian hierarchical approach to jointly fit models estimating of forcing, chilling and photoperiod sensitivity for each species and the effects of several dimensions of climate intensity and variability in the species ranges on these estimates. With this approach we 1) clarify the relationships between climatic variability across multiple scales of spatio-temporality, 2) identify the climate drivers that are more and less likely to drive selection on phenological cues and 3) compare variation in cue-use among and within species and between temperate Europe and North America. Our interrogation

of these relationships between climate and cue use not only clarifies the evolutionary drivers of phenoloical cues, 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

Statistical analysis

Coherance of climate variability

climate cue-use relationships

Dan write description of joint model

Intra vs. interspecific models

Cat

Results

Climate intensity and cue use

Overall, the mean forcing (GDDs) and chilling (Chill Portions) had weak effects on estimated cue use. In our full species models mean GDDs and had a weakly negative or neutral association with cue strength (GDD:Chill=X ,GDD:Force=Y, GDD:Photo=Z, (Fig. **??**)). The general sign of these relationships persisted in the continent subset models (Fig. **??** d),e),f)) with the exception of the relationship between mean GDDs and chilling for North American species which became positive (mean= Z, (Fig. **??** c)). Generally, there was high uncertainty around these estimates suggesting climate intensity is a poor predictor for cue use.

Coherance of spatio-temporal spring climate variability

The spatio-temporal coherence of spring climate variability and intensity varied across continent and scales. Generally climate intensity (mean GDDs in range mean Chill Portions in range and Mean GDDs to last frost) were well correlated with climate variability (Fig. 2a),b),c),d),h)) though strong differences can be observed between North American and Europe. Intra-annual, inter-annual and spatial variability in spring climate were also well correlated (Fig. 2e),f),g)), though the variability of spring climate in Europe was very low, suggesting that these correlation are likely more relevant in North America.

Climate variation and cue use

In our full models, our two measures of spring climate variability (GDD to last frost and STV), were weakly positively associated with forcing and photoperiod sensitivity and negatively associated with chilling sensitivity (Fig. 3a),b)). Generally, the was more uncertainly around our estimates of STV effects than GDD to last frost. However, our continent subset models shows different effect. Both STV and GDD to last frost are poorly estimate the European

6

models, and STV is also a poor predictor of cue use in North American models (Fig. 3d),e), f)). In the North America subset model variation in GDD to last frost increases sensistivity in all three cues (Chilling:X Forcing:Y Photoperiod:Z, (Fig. 3c))) suggesting there may be support for the climate variation hypotheses in North America where spring climate variation can be extreme.

Local adaptation of phenological cues

We detected limited population level variation in forcing and photoperiod cue sensitivity, though this within species variation was less substantial than among species variation(Fig. 4).

Discussion

1. Generally we found that the the climate-cue hypotheses were not well supported in our data.

2. Little evidence for climate intensity, and support for the climate variability hypothesis only in North America with one metric GDD to last frost.

3. This finding is inline with Zohners study, which favored variability and suggests as a result North America should have stronger cues.

4. We are not surprise GDD2lst frost is a better metric than STV.

5. We found that among species variation exceedes within species. But this suggest some levels of local adaptation which can muddy the signal.

6. Look at the maps, ranges are highly overlapping especially in Europe. Maybe this cliamte cues hypotheses only opperate across biomes.

7. While our analyses suggest the climate-cue relationships are murkey, on of our standout results are the differences between Europe and North America, in climate, cue strength and their relationship. Talk about the get stream. And maybe conenct to climate change here. IE if jet stream breaks, and EU varaiability increases, plants might not know what hit them

8. This tells us Analyzing data across continents may be a bad aproach and obscure inportant relationships. We see this too in our analyses experimental effects may be strongly dependent on where the experiment is done, so cross-continent syntheses are tricky.

9. Alternate hypotheses: 'Pioneer' species versus whatever the other term is (Laube paper), phylogeny.

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. Alterntaive explainations: A ton of hypotehses about community dynamics, phylogeny etc

References

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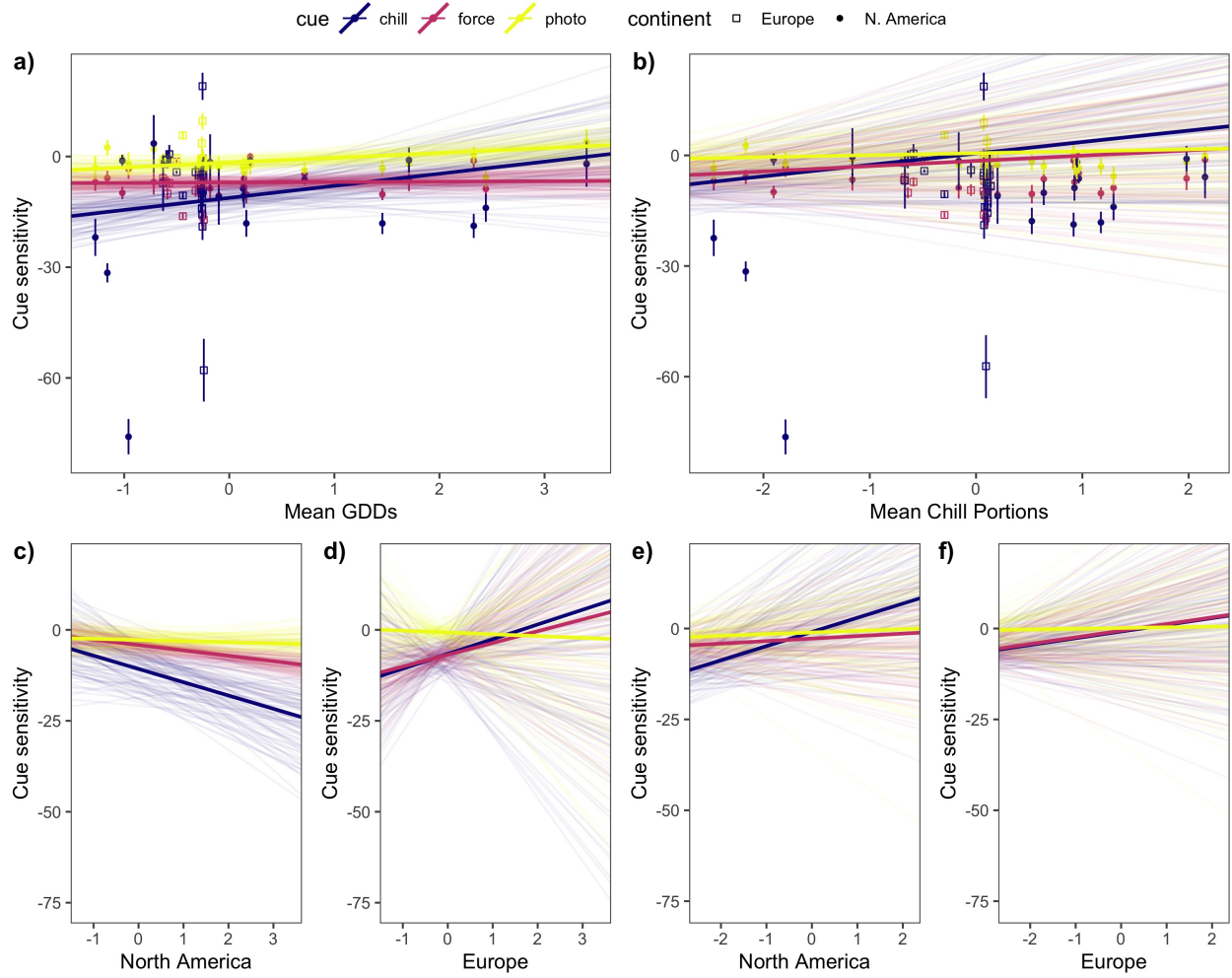
Figures

Figure 1: The effects of climate intensitives on the phenological sensitivity to chilling, forcing and photoperiod of temperatue woody species. Figure a) depicts the effects of mean GDDs on cue sensitivity for all 40 species in the study and b) depicts effects of chilling on cue sensitivity. All values on the x axis are standardized with zscoring for comparision across plots. The thick, bolded lines indicated the mean estimates of the effect of the climate variables on cue sensitivity estimates and the thinner lines represent 100 random draws from the posterior distrubrion of these estimates to characterize uncertainty. c) and d) depict the relationships between mean GDD and cue sensitivity and e) and f) the relationships between mean chilling and cue sensitivity for models run on only North American species or European species respectivey.
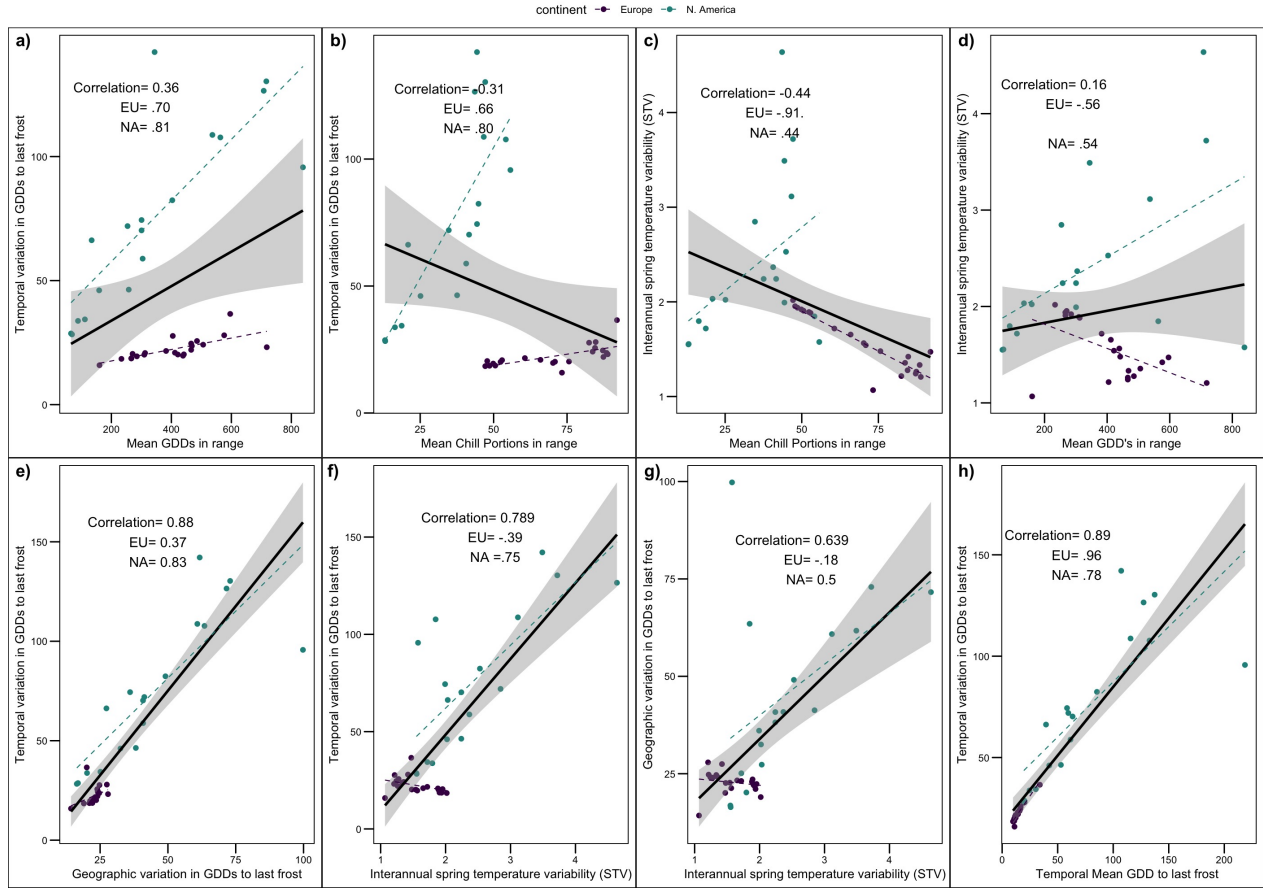
Figure 2: Corelations between spatio-temporal axes of climate varation and intesities in the full data set and across North American and European species ranges. a) and b) depicts correlation between inter-annual variation in growing degrees to last frost and mean growing degree days and mean levels of chilling in range respectively. c) and d) depicts correlation between interannual variation in mean spring temperature (STV) and mean growing degree days and mean levels of chilling in range respectively. e) demonstrate correlations between temporal and spatial inter-annual variation in growing degrees to last frost. f) and g) show the corelations between temporal and spatial variation in GDDs to last frost and STV respectively and h) the correlations between variation in GDDs to last frost and mean number of GDDs to last frost.
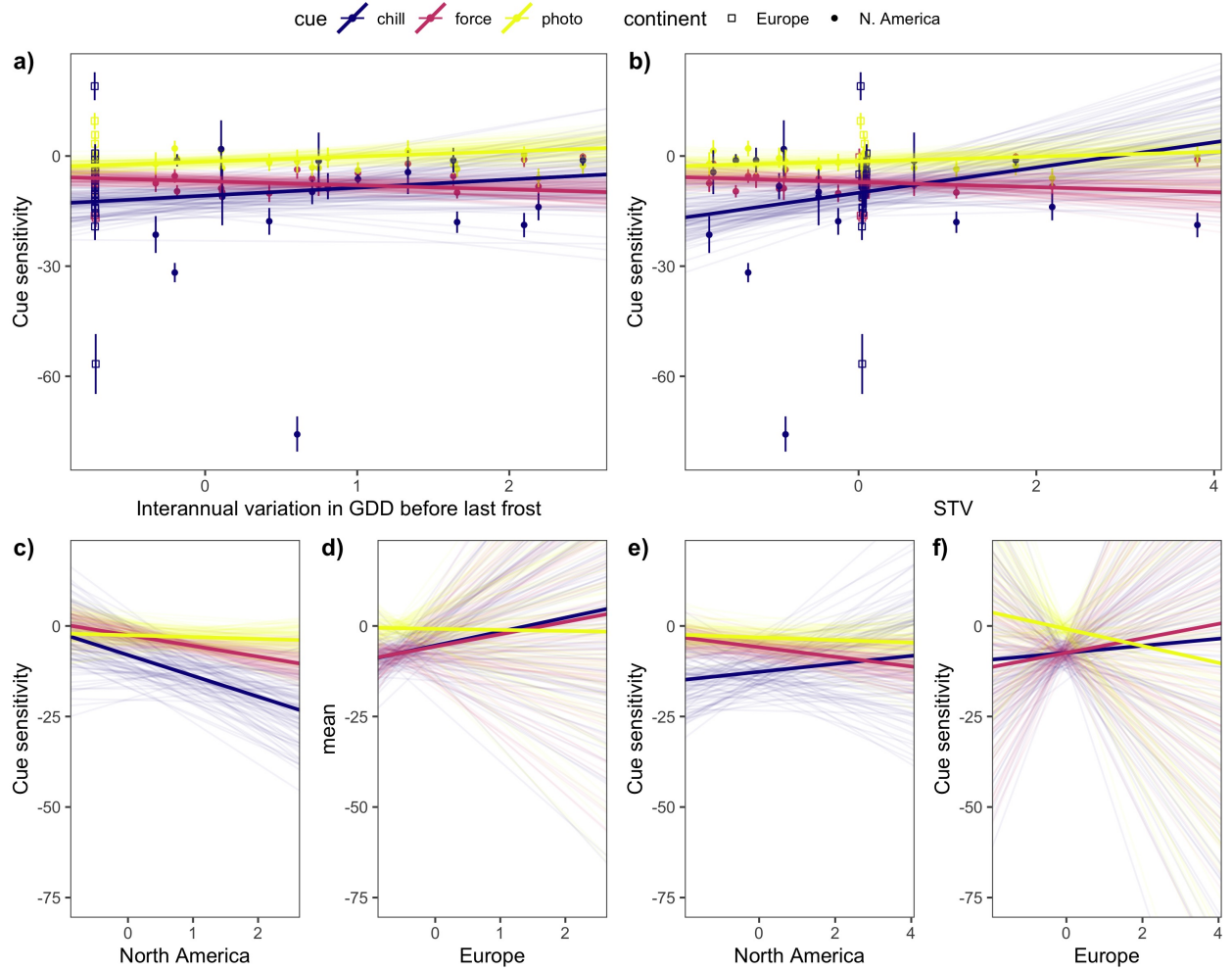
Figure 3: The effects of two measures of spring climate variabilitity on the phenological sensitivity to chilling, forcing and photoperiod of temperatue woody species. Figure a) depicts the effects of variability in number of growing degree days to last frost on cue sensitivity for all 40 species in the study and b) depicts effects of interannual mean spring temperature variation (STV) on cue sensitivity. All values on the x axis are standardized with zscoring for comparision across plots. The thick, bolded lines indicated the mean estimates of the effect of the climate variables on cue sensitivity estimates and the thinner lines represent 100 random draws from the posterior distrubrion of these estimates to characterize uncertainty. c) and d) depict the relationships between variation in GDDs to last frost and cue sensitivity and e) and f) the relationships between STV and cue sensitivity for models run on only North American species or European species respectivey.
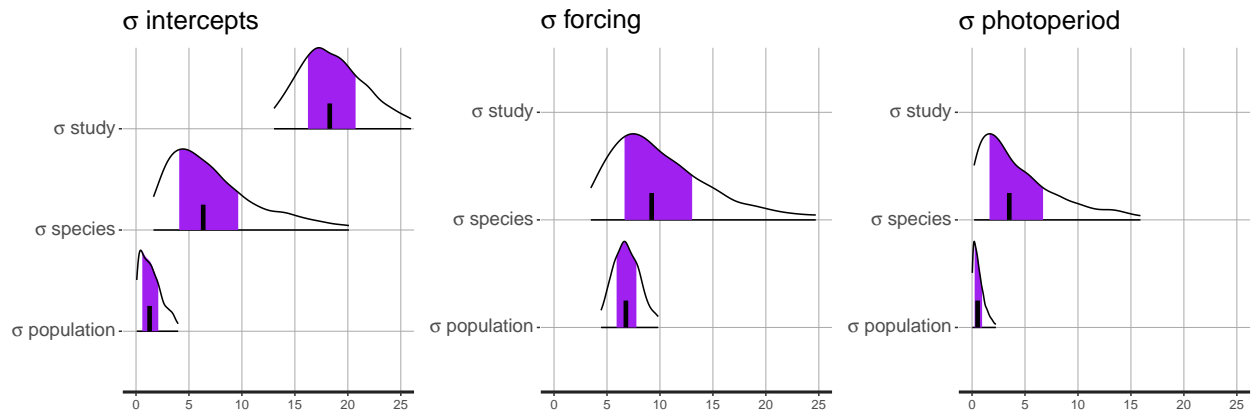
Figure 4: Interspecific variation exceeds intraspecific. Maybe Cat should write this?