

RH: Interactive cues and spring phenology

Concept paper on understanding interactive cues and climate change (with growth chamber studies)

- (1) How interactive cues will shape climate change responses
- (2) Limiting cues: How spring warming, winter chilling and daylength will shape climate change responses
- (3) Spring warming, winter warming or daylength: What cue will be most limiting in future tree phenology?

THE LAB^{1,2}

¹ *Arnold Arboretum of Harvard University, 1300 Centre Street, Boston, Massachusetts, 02131, USA*

² *Organismic & Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts, 02138, USA*

³ *Forest & Conservation Sciences, Faculty of Forestry, University of British Columbia, 2424 Main Mall, Vancouver, BC V6T 1Z4*

Corresponding author: XX, see ^{1,2} above ; E-mail:.

Abstract

Climate change has shifted plant phenology globally, with average shifts of 4-6 days/°C and some species shifting several weeks. Globally, such shifts have been some of the most reported and most predictable biological impacts of climate change. This predictability comes from decades of research, which have outlined the major cues that drive most studied plant phenology: temperatures (including spring warming and winter chilling) and daylength. Further simplifying predictions, spring temperatures are often the dominant cue in nature, making linear models of heat sums often excellent at predicting interannual variation in phenology. Yet as climate change has marched on, new research has uncovered failures to predict the current observed changes, with many shifts appearing more muted over certain time periods or in certain locations. Here we argue that such inaccurate predictions are most likely due to simple models that neglect to consider other major cues—especially winter chilling and daylength, which moderate and shape plant phenological responses to spring warming. We highlight how over 60 years of research in controlled environments can improve predictions for when, where and how the interactive effects of other cues will impact simple linear predictions. Finally, we discuss how a new generation of controlled environment experiments could rapidly improve our predictive capacity for woody plant phenology in coming decades.

Main message (and, really, it's important): If you want to project climate change impacts, you need to focus on relevant changes in all three cues. The relevant changes part is about comparing cues, the all three cues is about interactive cues.

Keywords: phenology, climate change, spring warming, forcing, chilling, daylength, photoperiod, non-linear responses, leafout, budburst

Some to do items

1. Need to double-check how I count cues for checking INTERACTIONS!
2. Can we show an example of a double-cue non-linearity (Flynn data?) ...
3. Add details on exactly how figure 1 was created.
4. See question in 4d.
5. What figures do we really need/want in paper?
6. Check 5d ... do 43% of the studies really vary photo and force?

Take home messages

1. Current studies are relevant for some single cues ...
2. Interactive cues
3. Long-term studies should work harder to integrate experimental results...

OUTLINE

1. Introduction
 - (a) Shifts in spring phenology are one of the most reported and most predictable changes with climate change
 - i. Review the shifts across space and time and how coherent they are
 - ii. For example... Schwartz (1997); Menzel et al. (2003, 2006); Delpierre et al. (2009); Ellwood et al. (2013); Jochner et al. (2013); Hereford et al. (2017)
 - (b) Recently, however, predictions have started to fail in certain places or over certain time periods
 - i. Some examples: Yu et al. (2010); Fu et al. (2015)
 - ii. The main hypothesis for this failure is that most observational studies have ignored cues beyond simple spring warming ones (Chaine et al. 2016)
 - (c) There has been a lot of focus on spring warming but really it's more complicated
 - i. For many species three major cues drive spring phenology: forcing (spring warming), chilling (winter cool temperatures), daylength
 - ii. These cues may create critical non-linear responses that most current methods cannot predict.

So, the models we have are all linear ... but, the Flynn work suggests that chilling levels off at some point so we could do a simple hinge plot maybe? Linear effect of chill + force until chill met, then just force? Or better to do bucket model – that would be linear effect of chill (endo dormancy) then linear effect of force (eco) ... could also

- (d) However, measuring these cues and thinking about how they will interactively produce future phenology is hard because:
 - i. They vary across species (and possibly within species across the range, but see below) (Vitasse et al. 2009; Harrington and Gould 2015)
 - ii. They are expected to interact; cues may compensate for other cues; meaning they mask one another (e.g., chilling cue not fully being met could look like a photoperiod requirement that has not been met) *Isabelle says ‘for me this is two different things’ – so be careful of when we mean biologically (as in, what’s happening physiologically) and statistically (i.e., an interaction)
 - iii. They are hard to measure.
 - iv. To some extent (because of how they interact), we haven’t really had to measure these other cues to get decent predictions for lots of places and years
- (e) But if evidence is rising that these cues are critical, how do we integrate them more into phenological research? Step 1 is clearly to figure out how to robustly measure them.
 - i. Methods especially lame at understanding these cues (and thus predicting non-linearities): models from long-term observational data ... and other methods that lead to correlated cues.
 - ii. Comment on the two issues at play here: the data type (e.g., long-term) versus the model type (e.g., linear and sans interactions?)
 - iii. The one method designed to look at all these cues is controlled environment (generally growth chamber) studies (Nagano et al. 2012; Satake et al. 2013)
- (f) Growth chamber studies
 - i. Can manipulate all three cues (and even more, humidity etc. nod?)
 - ii. Can be designed to tease out interactions (unlike other methods)
 - iii. Have been done *forever*. But oddly, never really reviewed.
 - iv. ...and are often poorly integrated into current climate change literature. Including debates where they are critical, like about photoperiod.
- (g) Our aim is to:
 - i. *Briefly* review how three major phenological cues for woody plant phenology will shift in coming decades with anthropogenic climate change (check Primack et al. (2015))
 - ii. Review of the three major phenological cues from growth chamber studies over the past 60 (70?) years to understand how much of the cue-space has been studied
 - iii. Compare treatments from controlled environment studies to predicted shifts in cues with climate change.

- iv. Show how growth chamber studies can be best designed to better understand these interactive cues (paths forward).
- (h) We focus on woody species ...
 - i. Research in the cues underlying phenology has been especially strong in model systems (e.g., *Arabidopsis*, *Populus*) and crops (Cesaraccio et al. 2004)—with the exact phenophase of interest varying (potentially by a species' life history: more focus on germination and flowering in *Arabidopsis*, and more on leafout and budset in *Populus*).
 - ii. Our focus here is on leafout, and thus we focus on woody species phenology: for which leafout has been widely studied across species, though much of what we say could apply to non-woody species and/or other phenophases with underlying similar cues.
- 2. Why do species have multiple cues? To understand this, it helps to think about the environmental variation a species experiences: across years, and across its range
 - (a) In the spring there is selection for species to track the start of resources, and thus they need cues that work across the interannual variation in climate *across a species' range* ... either through plasticity and/or local adaptation
 - (b) Unlike budset phenology, research suggests spring phenology can be fairly plastic (without high local adaptation of cues across a range); this means species will ideally use a set of cues that work across their range (Liepe et al. 2016), though there is some variation in the importance of each cue across a range (e.g., chilling in coastal versus continental, check also Legave et al. (2013))
 - (c) Thus, cues are adapted to high climate variation (spatially and temporally).
 - (d) This is why most temperate species are hypothesized to have responses to all three cues: forcing, chilling, photoperiod. And that at the extremes, these cues are expected to be non-linear (especially photo and chill), so they may not often show up in long-term data.
- 3. Review how cues will shift with climate change (here we maybe show the figures that Nacho has produced for two PEP725 spp., See Fig. 1, or save for later)
 - (a) Forcing: the world will get warmer
 - i. Higher altitude and arctic places will warm more
 - ii. Give range of warming depending on different scenarios
 - iii. Minima (night-time temps) generally warm more than maxima (but not everywhere, see what Yann mentioned). Note Piao et al. (2015)- found that daytime forcing temperatures (Tmax) are more important for leaf out than nighttime temperatures (Tmin).

- iv. Different seasons may warm differently
 - (b) Chilling, see forcing but ...
 - i. Chilling only occurs between certain temps so some places accumulate more chilling with warming
 - ii. And there is so much we don't know about how chilling works and interacts with forcing (sequential model, parallel models etc.)
 - (c) Photoperiod: Shifts with phenology
 - i. Changes in forcing and chilling will alter the photoperiod that matters so to speak
 - ii. Note that although daylengths themselves won't change with climate change, the photoperiods experienced by organisms are likely shift as ranges shift and phenology shift (cite our other paper?)
 - (d) Together these cues may create non-linearities. **Two types of non-linearities**, non-linearities in one cue and non-linearities produced by cue interactions. We suggest briefly where these may be expected:
 - i. If we know where a non-linearity in a response to a cue is (e.g., from experiments of models we know that the response to photoperiod gets bigger after 16 hours), then wherever you're near that on a range, you should expect bigger effects of that cue. *Should we add a figure showing this for forcing or chilling?
 - ii. Where chilling will change to above versus below the threshold that plants can sense
 - iii. Something about non-linearities from interactive cues. Maybe we can just say that these are perhaps the hardest to predict, but may be most important?
4. Growth chamber studies should help predict both these non-linearities. This is especially useful for forecasting if they are designed in a range relevant to current and future conditions: Compare treatments from controlled environment studies to predicted shifts in cues with climate change: **Part I: Review of the three major phenological cues from growth chamber studies over the last 67 years**
- (a) Be sure to note that most studies were *not* done for climate change research, they were done for fundamental science or agricultural/forestry purposes
 - (b) Studies have been done across the globe ... (with more in Europe) and across the decades
 - i. Fig: Map of studies, coded by datasetID and species n , see Fig. 2
 - ii. Fig: Number of studies by year (OSPREE), see Fig. 3
 - (c) For each of the three cues:
 - i. 56% manipulated forcing; 55% manipulated photoperiod, 33% manipulated chilling

- ii. Variation across latitude: forcing and chilling declines 0.1C per degree latitude (for forcing, min is -0.12, for max it's -0.08, see Fig 4; for chilling it's -0.1 for min and -0.07 for max); max photo increases with latitude (0.08 hr per degree);
 - iii. Explain drawback of one-cue ... you don't see interactions *and* I think you bias yourself to mainly seeing variation in the one cue so you cannot compare the relative effects of multiple cues
 - iv. Maybe: Variation across and hemispheres? continents, time and species?
 - v. Maybe: Say something about material (seeds/saplings/cuttings)? Can we tie to relevance of predicting future forest communities or such?
- (d) X% of studies manipulated which interacting cues? (i.e., how many studies manipulate 1 cues, 2 cues, 3 cues ... of those manipulating 1 cue, what is the breakdown by cue etc.) ... 43% manipulated forcing and photo, only 10% manipulated chilling and forcing or photo (9% for chill x photo; 10% for chill x force), see Fig. 5
5. Compare treatments from controlled environment studies to predicted shifts in cues with climate change: **Part II: What cues will be most limiting with climate change? How do controlled environment studies compare?**
- (a) Consider both the range of a species and the climate change projections ...
 - i. Take each PEP725 datapoint within our selected species' range and calculate:
 - A. Do we really have negative forcing in OSPREE? (See Fig. 1)
 - B. Experiments have done a good job of testing chilling compared to climate change projections, covers full range and overshoots a bit ... (See Fig. 1) ¹
6. Paths forward (showcase how growth chamber studies can be best designed to better understand these interactive cues in regards to climate change forecasting)
- (a) If you want work to be most relevant to climate change, then consider the following when designing experiments:
 - i. The cues with the current vs. future range of a species (as we did above) to inform experimental range
 - ii. If you don't work within the range or projected cue range limits of a species, then consider working on informative extremes to help identify where single-cue nonlinearities exist... but some extremes (e.g., chilling) are difficult to reproduce in controlled environments (and this is something we technologically need to improve)
 - (b) Manipulating more than one cue may be most useful, esp. if we want to understand interactive cues and advance comparisons with long-term data

¹We used daily min/max, as they're most directly comparable to OSPREE.

- (c) Major need to better understand deviations in long-term data are: better non-linear models for more species. How best to do this?
 - i. Studies using only long-term observational data have already improved in being clear about correlations in predictor variables (e.g., chilling, forcing and daylength often covary). This means we generally cannot robustly identify other cues through statistical modeling and need alternative approaches...
 - ii. A better option than just long-term data are more efforts to integrate long-term data with growth chamber studies (Caffarra et al. 2011; Nagano et al. 2012; Satake et al. 2013; Ford Kevin et al. 2016; Chuine and Regniere 2017)
 - A. Studies that test the extremes are needed to parameterize models (ideally you need to know where the zeros are) (Chuine and Regniere 2017)
 - B. Traditional methods to hold-out data and test how well the model performs
 - C. Use growth chamber studies to test model predictions, especially in future climate scenarios where non-linearities are predicted, and vice versa (see Nagano et al. 2012)
 - D. Improving models means more back-and-forth work between developing models based on both long-term data and experiments, then testing predictions with new experiments and as newer observational data are generated (i.e., more years and also data from new locations) ... (Nagano et al. 2012; Satake et al. 2013)
 - (d) Building species-rich predictions ...
 - i. Given how complicated this all sounds, how do we build up to multi-species predictions?
 - ii. Need more efforts to combine data
 - iii. Introduce Bayesian hierarchical modeling within this framework
 - iv. And need more efforts to publish studies in a way that makes synthesis possible ...
 - v. Studies not interested in climate change forecasting can still contribute—with little effort—to progress in this area by: Reporting all cues (even the ones you don't measure) so they can be used in modeling efforts.
7. Wrap-up: Climate change: it means all that work on phenology comes due ... now!
- (a) If we could better harness the power of growth chamber studies it could... transform our fundamental understanding of this important aspect of plant biology and forecasting
 - (b) Rule out or in hypotheses to explain observed discrepancies (move away from trying to tease out cues using only correlated long-term data)

- (c) Contribute to more models being developed and improved, which could contribute to global land surface models, community predictions etc.
- (d) While understanding, modelling and predicting interactions among cues and their effects on phenology is challenging, any advances on this should yield more accurate predictions, with valuable implications to more realistically assess the effects of climate change on plant biodiversity, including agricultural and forest species.

Examples of how cues interact:

1. OSPREE studies found that additional chilling, or even simply sufficient chilling, could lower the photoperiod requirement but when the chilling requirement wasn't fulfilled, increased photoperiod could compensate for the lack of chilling (Nienstaedt 1966; Myking and Heide 1995; Falusi and Calamassi 1996; Hawkins and Dhar 2012)

FIGURES

1. PEP725 spp. 1980 figures
2. PEP725 spp. Future figures
3. Number of studies by year (OSPREE) *Other ideas?! Such as, number of species studied by year. Show crops or remove or show separately?*
4. Map of studies, color coded or such by which of the three cues they manipulated
5. Variation in treatments across space (photo/chill/force)
6. Variation in treatments across time (graph with year on x -axis or divide time in half or such?)
7. Not a figure, but analysis-related: X% of studies manipulated which interacting cues? (i.e., how many studies manipulate 1 cues, 2 cues, 3 cues ... of those manipulating 1 cue, what is the breakdown by cue etc.)

*

References

- Caffarra, A., Donnelly, A., and Chuine, I. (2011). Modelling the timing of *Betula pubescens* budburst. II. Integrating complex effects of photoperiod into process-based models. *Climate Research*, 46(2):159–170. Times Cited: 2 Caffarra, Amelia Donnelly, Alison Chuine, Isabelle.
- Cesaraccio, C., Spano, D., Snyder, R. L., and Duce, P. (2004). Chilling and forcing model to predict bud-burst of crop and forest species. *Agricultural and Forest Meteorology*, 126(1-2):1–13.
- Chuine, I., Bonhomme, M., Legave, J. M., de Cortazar-Atauri, I. G., Charrier, G., Lacointe, A., and Ameglio, T. (2016). Can phenological models predict tree phenology accurately in the future? the unrevealed hurdle of endodormancy break. *Global Change Biology*, 22(10):3444–3460.
- Chuine, I. and Regniere, J. (2017). Process-based models of phenology for plants and animals. *Annual Review of Ecology, Evolution, and Systematics*, 48:159–182.
- Delpierre, N., Dufrene, E., Soudani, K., Ulrich, E., Cecchini, S., Boe, J., and Francois, C. (2009). Modelling interannual and spatial variability of leaf senescence for three deciduous tree species in france. *Agricultural and Forest Meteorology*, 149(6-7):938–948.

- Ellwood, E. R., Temple, S. A., Primack, R. B., Bradley, N. L., and Davis, C. C. (2013). Record-breaking early flowering in the eastern united states. *Plos One*, 8(1). Ellwood, Elizabeth R. Temple, Stanley A. Primack, Richard B. Bradley, Nina L. Davis, Charles C.
- Falusi, M. and Calamassi, R. (1996). Geographic variation and bud dormancy in beech seedlings (*fagus sylvatica* l). In *Annales des Sciences forestières*, volume 53, pages 967–979. EDP Sciences.
- Ford Kevin, R., Harrington Constance, A., Bansal, S., Gould Peter, J., and St. Clair, J. B. (2016). Will changes in phenology track climate change? a study of growth initiation timing in coast douglasfir. *Global Change Biology*, 22(11):3712–3723.
- Fu, Y. S. H., Zhao, H. F., Piao, S. L., Peaucelle, M., Peng, S. S., Zhou, G. Y., Ciais, P., Huang, M. T., Menzel, A., Uelas, J. P., Song, Y., Vitasse, Y., Zeng, Z. Z., and Janssens, I. A. (2015). Declining global warming effects on the phenology of spring leaf unfolding. *Nature*, 526(7571):104–107.
- Harrington, C. A. and Gould, P. J. (2015). Tradeoffs between chilling and forcing in satisfying dormancy requirements for pacific northwest tree species. *Frontiers in Plant Science*, 6:120.
- Hawkins, C. D. and Dhar, A. (2012). Spring bud phenology of 18 *betula papyrifera* populations in british columbia. *Scandinavian Journal of Forest Research*, 27(6):507–519.
- Hereford, J., Schmitt, J., and Ackerly, D. D. (2017). The seasonal climate niche predicts phenology and distribution of an ephemeral annual plant, *mollugo verticillata*. *Journal of Ecology*, 105(5):1323–1334.
- Jochner, S., Caffarra, A., and Menzel, A. (2013). Can spatial data substitute temporal data in phenological modelling? a survey using birch flowering. *Tree Physiology*, 33(12):1256–1268.
- Legave, J. M., Blanke, M., Christen, D., Giovannini, D., Mathieu, V., and Oger, R. (2013). A comprehensive overview of the spatial and temporal variability of apple bud dormancy release and blooming phenology in western europe. *International Journal of Biometeorology*, 57(2):317–331.
- Liepe, K. J., Hamann, A., Smets, P., Fitzpatrick, C. R., and Aitken, S. N. (2016). Adaptation of lodgepole pine and interior spruce to climate: implications for reforestation in a warming world. *Evolutionary Applications*, 9(2):409–419.
- Menzel, A., Jakobi, G., Ahas, R., Scheifinger, H., and Estrella, N. (2003). Variations of the climatological growing season (1951–2000) in Germany compared with other countries. *International Journal of Climatology*, 23(7):793–812.
- Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kubler, K., Bissolli, P., Braslavska, O., Briede, A., Chmielewski, F. M., Crepinsek, Z., Curnel, Y., Dahl, A.,

- Defila, C., Donnelly, A., Filella, Y., Jactza, K., Mage, F., Mestre, A., Nordli, O., Penuelas, J., Pirinen, P., Remisova, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A. J. H., Wielgolaski, F. E., Zach, S., and Züst, A. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology*, 12(10):1969–1976.
- Myking, T. and Heide, O. (1995). Dormancy release and chilling requirement of buds of latitudinal ecotypes of *betula pendula* and *b. pubescens*. *Tree physiology*, 15(11):697–704.
- Nagano, A. J., Sato, Y., Mihara, M., Antonio, B. A., Motoyama, R., Itoh, H., Nagamura, Y., and Izawa, T. (2012). Deciphering and prediction of transcriptome dynamics under fluctuating field conditions. *Cell*, 151(6):1358–1369.
- Nienstaedt, H. (1966). Dormancy and dormancy release in white spruce. *Forest Science*, 12(3):374–384.
- Piao, S. L., Tan, J. G., Chen, A. P., Fu, Y. H., Ciais, P., Liu, Q., Janssens, I. A., Vicca, S., Zeng, Z. Z., Jeong, S. J., Li, Y., Myneni, R. B., Peng, S. S., Shen, M. G., and Penuelas, J. (2015). Leaf onset in the northern hemisphere triggered by daytime temperature. *Nature Communications*, 6.
- Primack, R. B., Laube, J., Gallinat, A. S., and Menzel, A. (2015). From observations to experiments in phenology research: investigating climate change impacts on trees and shrubs using dormant twigs. *Annals of Botany*, 116(6):889–897. Primack, Richard B. Laube, Julia Gallinat, Amanda S. Menzel, Annette Menzel, Annette/B-1105-2013 1095-8290 Si.
- Satake, A., Kawagoe, T., Saburi, Y., Chiba, Y., Sakurai, G., and Kudoh, H. (2013). Forecasting flowering phenology under climate warming by modelling the regulatory dynamics of flowering-time genes. *Nature Communications*, 4.
- Schwartz, M. D. (1997). Spring index models: An approach to connecting satellite and surface phenology. In Lieth, H. and Schwartz, M. D., editors, *Phenology in Seasonal Climates I*, pages 22–38. Backhuys Publisher, Leiden, The Netherlands.
- Vitasse, Y., Delzon, S., Bresson, C. C., Michalet, R., and Kremer, A. (2009). Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, 39(7):1259–1269.
- Yu, H. Y., Luedeling, E., and Xu, J. C. (2010). Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. *Proceedings of the National Academy of Sciences of the United States of America*, 107(51):22151–22156. Yu, Haiying Luedeling, Eike Xu, Jianchu.

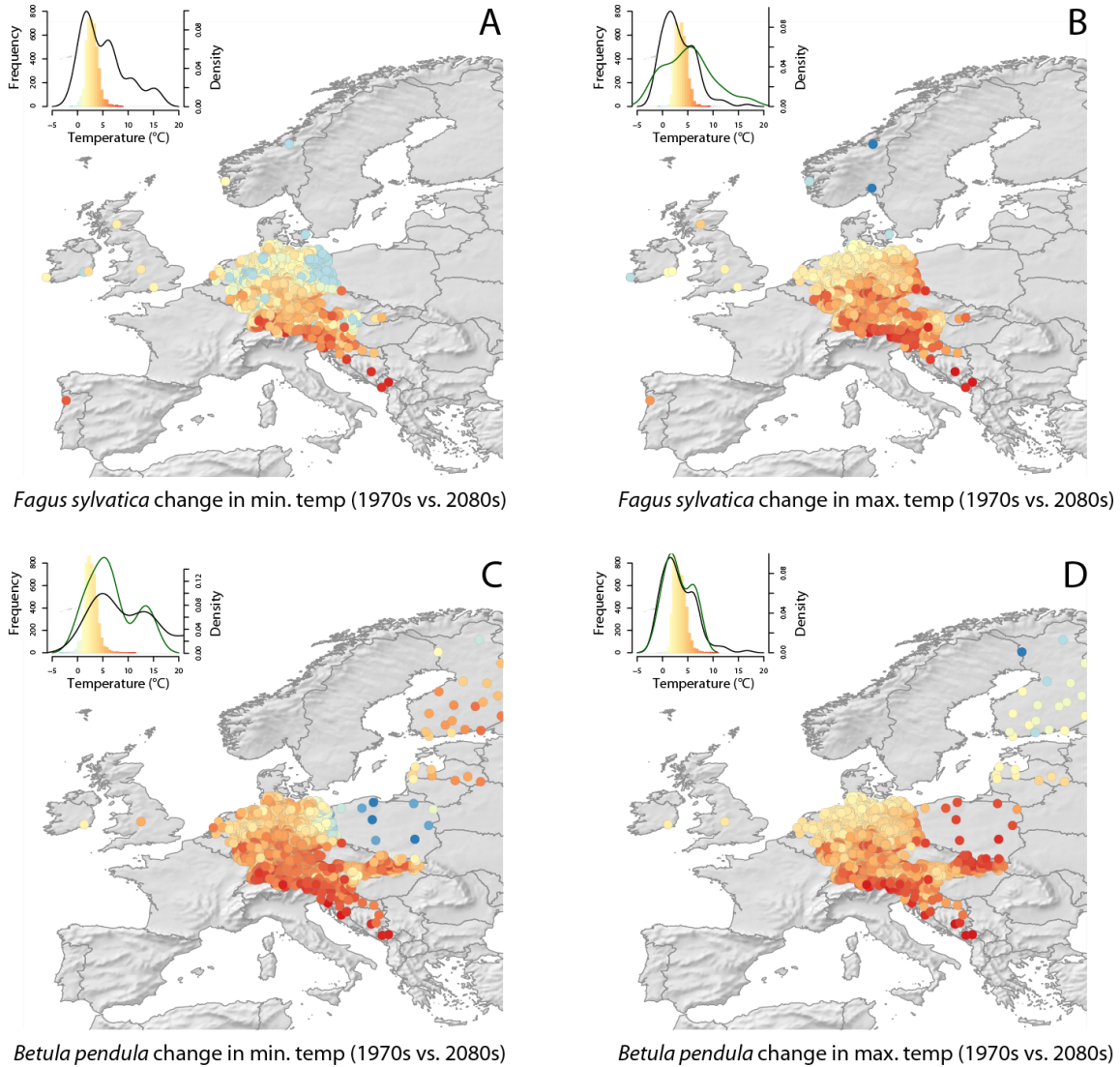
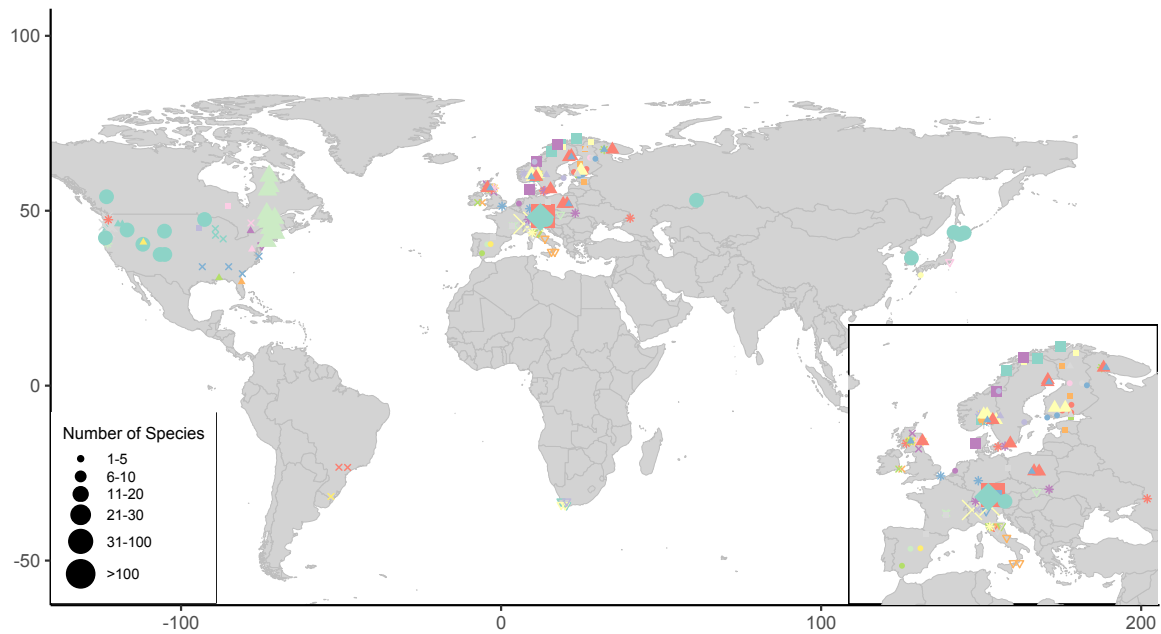


Figure 1: Predicted changes in temperatures relevant to chilling (A, C) and forcing (B, D) compared to a 1970s baseline shown for two species: *Fagus sylvatica* (A-B) and *Betula pendula*. Points represent a PEP725 site with XX data. Inlay plots in the upper left-hand corner of each plot show a histogram of the predicted changes in temperature overlaid with densities of the chilling (A, C) and forcing (B, D) treatments (green lines show the treatments for that exact species, while black lines show across all species; note that for *Fagus sylvatica* there are no chilling treatments of differing temperatures).



DatasetID			
ashby62 ; 3	gansert02 ; 1	lamb37 ; 1	ruesink98 ; 1
basler12 ; 28	ghelardini10 ; 6	laube14a ; 36	Sanz-Perez09 ; 2
basler14 ; 4	gianfagna85 ; 1	laube14b ; 9	sanzperez10 ; 3
biasi12 ; 2	gomory15 ; 2	li05 ; 3	schnabel87 ; 2
boyer ; 4	granhus09 ; 1	linkosalo06 ; 1	skuterud94 ; 6
caffarra11a ; 4	guak98 ; 1	man10 ; 1	sogaard08 ; 1
caffarra11b ; 1	guerriero90 ; 1	morin10 ; 3	sonsteby13 ; 8
calme94 ; 3	Heide03 ; 3	myking95 ; 6	sonsteby14 ; 5
campbell75 ; 6	heide05 ; 4	myking97 ; 1	spann04 ; 1
cannell83 ; 2	heide08 ; 5	myking98 ; 3	spiers74 ; 1
charrier11 ; 3	heide11 ; 3	nienstaedt66 ; 14	swartz81 ; 1
chavarria09 ; 1	heide12 ; 3	nishimoto95 ; 3	viheraarnio06 ; 2
cook00b ; 2	heide15 ; 1	pagter15 ; 2	webb78 ; 3
cook05 ; 2	heide93 ; 9	partanen01 ; 3	worrall67 ; 12
cronje03 ; 1	heide93a ; 5	partanen98 ; 3	yazdaniha64 ; 1
falusi03 ; 1	howe95 ; 2	pettersen71 ; 1	zohner16 ; 144
falusi90 ; 1	jones12 ; 3	ramos99 ; 1	
falusi96 ; 5	junttila12 ; 6	rinne94 ; 1	
falusi97 ; 2	karlsson03 ; 2	rinne97 ; 1	

Figure 2: Overview of the data across space.

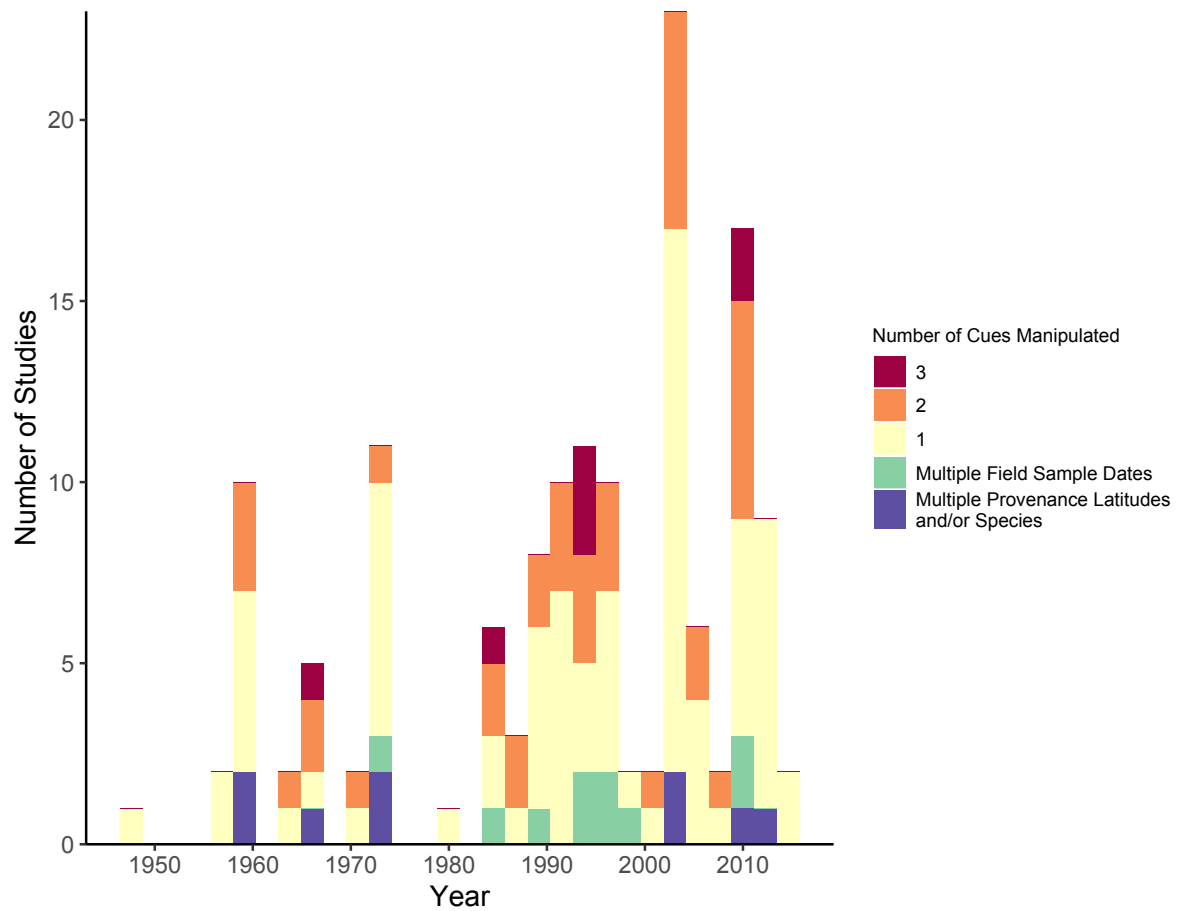


Figure 3: Cues manipulated over time.

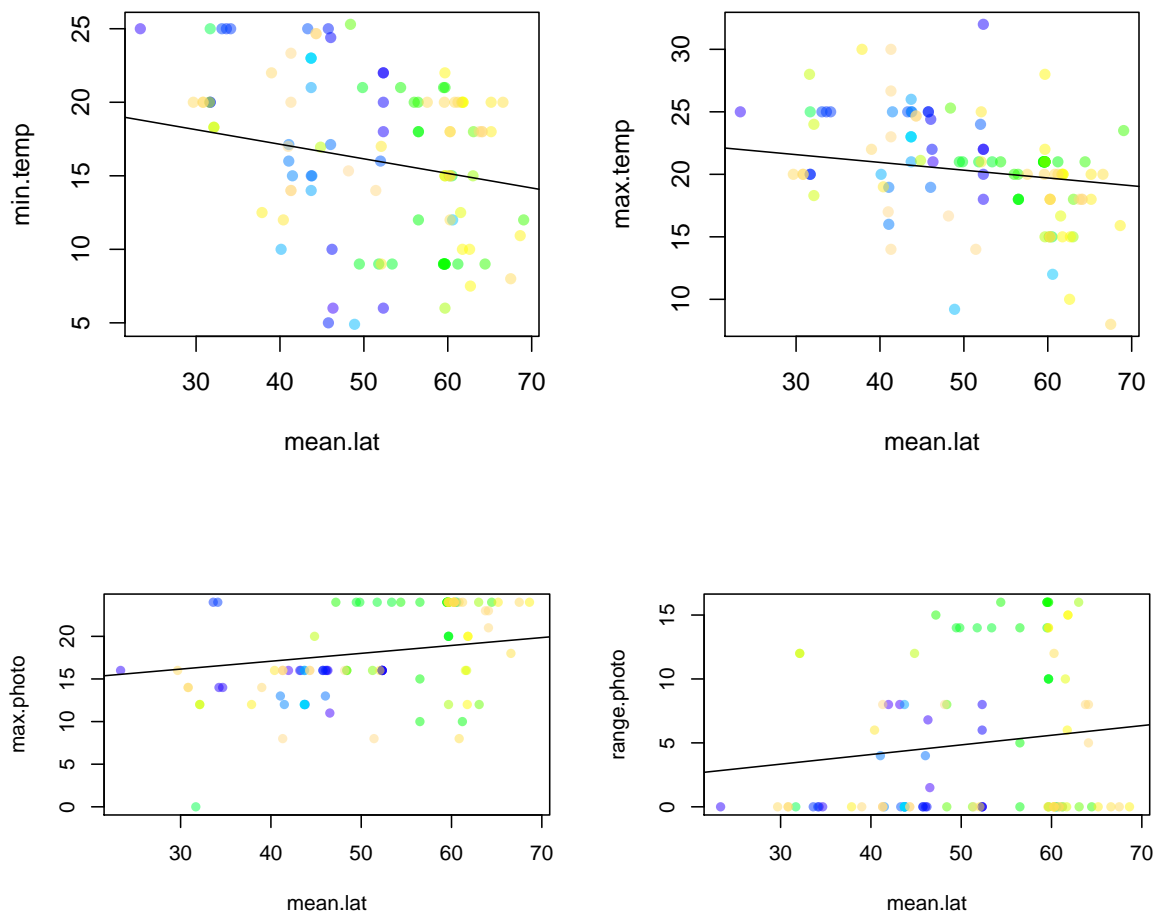


Figure 4: One correlation with latitude plot? Or more?

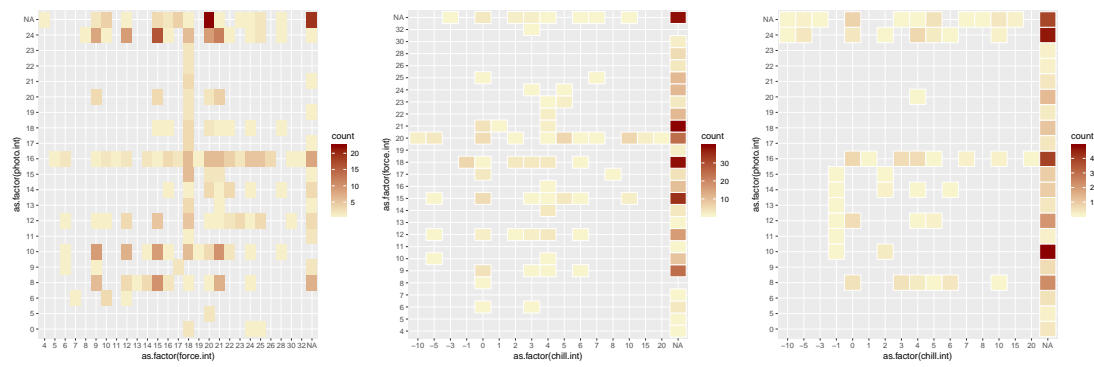


Figure 5: Heat maps.