Flowering phenology in lodgepole pine

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Lodgepole pine flowering biology

In spring

- Male strobili shed pollen
- Female strobili capture pollen

Wind pollinated

Phenology matters

- Gene flow
  - assortative mating
  - (local) adaptation
  - clinal variation
- Seed orchard management
- Tree breeding
- Assisted migration

What controls the timing of flowering phenology in lodgepole pine?

- Chilling accumulation
- Forcing accumulation
- Genetics

- Assume met
- assume > 5 °C
- Is there clinal variation?

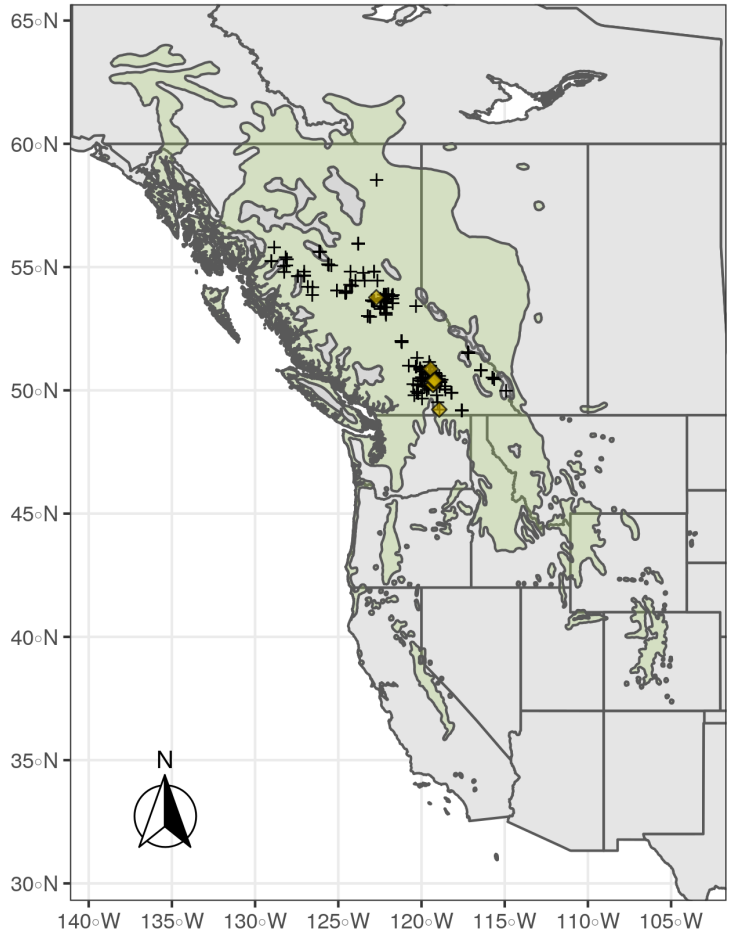
Data

- 748 clones of 259 genotypes
- grown in 7 seed orchards across BC
- flowering state recorded every few days over a one day to several week period
- 15 total years of data collection

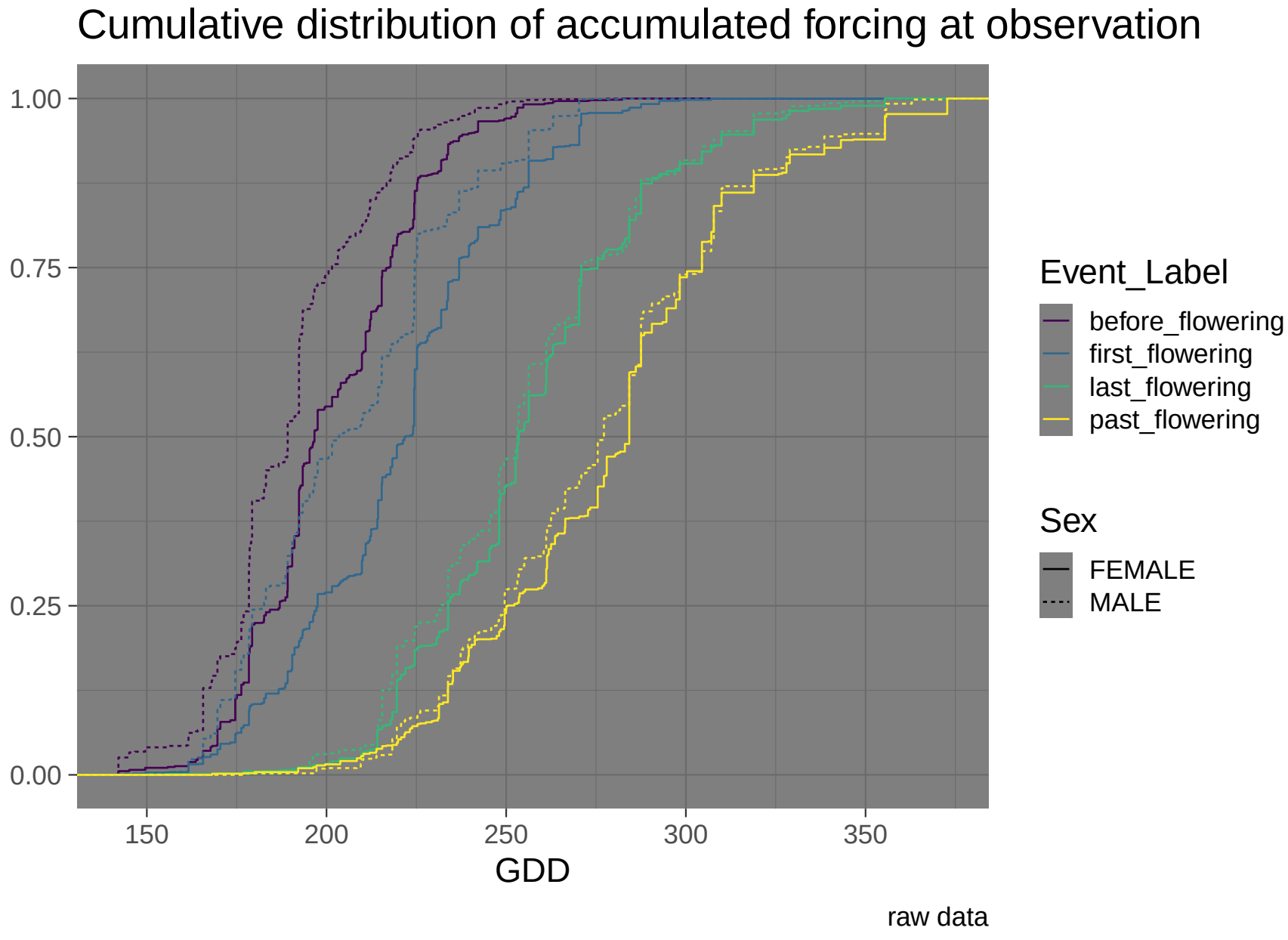
Provenance

- seeds and scions from 143 natural stands
- grafted onto rootstock to create a clone bank
- clone bank scions selected based on superior growth, form

Map


65◦N
60◦N
55◦N
50◦N
45◦N
40◦N
35◦N
30◦N
140◦W
135◦W
130◦W
125◦W
120◦W
115◦W
110◦W
105◦W
N

Data


Cumulative distribution of accumulated forcing at observation
1.00
0.75
0.50
0.25
0.00
150
200
250
300
350
GDD
raw data
Event_Label
before_flowering
first_flowering
last_flowering
past_flowering
Sex
FEMALE
MALE

How much forcing?

- 4 models
  - Begin (male) pollen shed
  - End (male) pollen shed
  - Begin (female) receptivity
  - End (female) receptivity
- Thermal time - transferable
- Test for provenance climate effect - MAT
- Account for variance due to site, year, genotype, and clone
- Account for unbalanced and censored data

Likelihood model

Likelihood of forcing observations would have a normal distribution

$$f_i \sim \mathrm{Normal}(\phi_i, \sigma)$$

But all of my data is censored.

Event	Sex	interval	left	right
begin	FEMALE	0.63	0.37	NA
begin	MALE	0.35	0.65	NA
end	FEMALE	0.47	NA	0.53
end	MALE	0.48	NA	0.52

Likelihood model - for censored data

So we assume an underlying normal distribution that we're observing badly.

- Left censored start data (hazard function)

$$\Pr[f_i < U] = \int_{\infty}^{U} \text{Normal}(y \mid \phi_i, \sigma) dy$$

- Right censored end data (survival function)

$$\Pr[f_i > L] = \int_{L}^{\infty} \text{Normal}(y \mid \phi_i, \sigma) dy$$

- Interval censored data

$$\Pr[L > f_i > U] = \int_{L}^{U} \text{Normal}(y | \phi_i, \sigma) dy$$

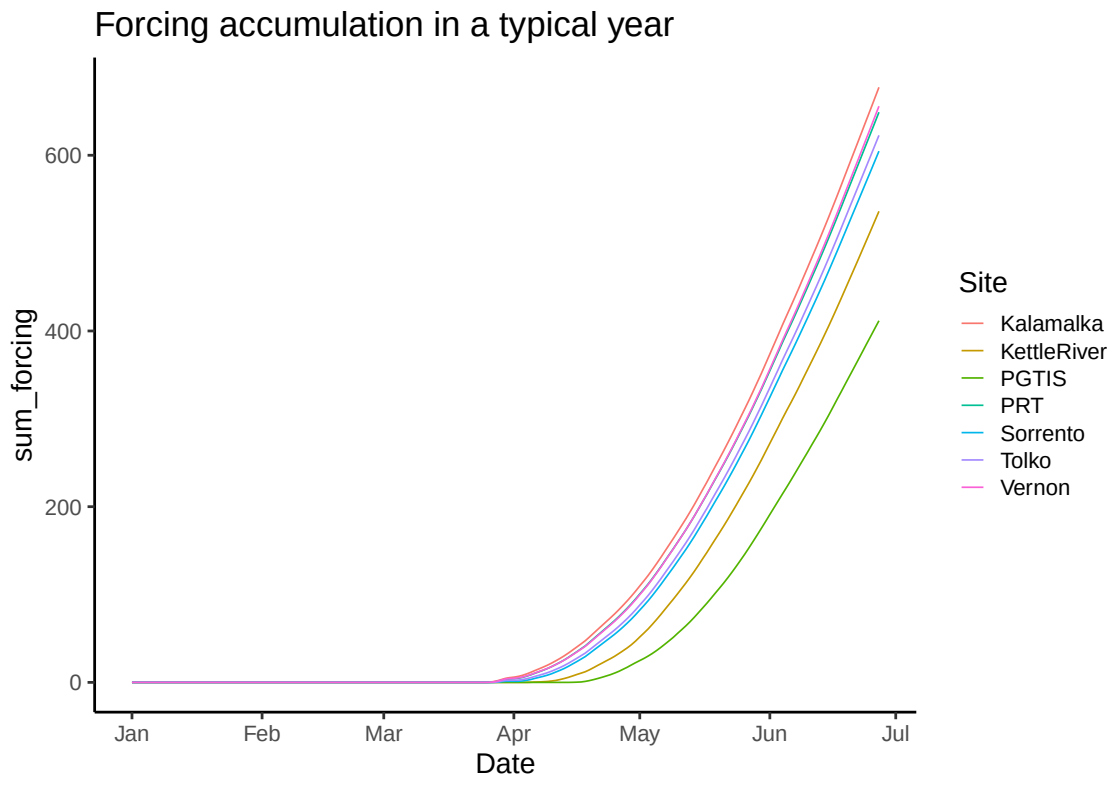
Modeling the mean

$$\phi_i = \alpha + \beta MAT + \delta_{Site,i} + \delta_{Year,i} + \delta_{Clone,i} + \delta_{Ramet,i}$$

- α: Overall mean forcing requirement
- β: Provenance climate effect using MAT as covariate
- δ: Offsets from the overall mean based on site, year, clone, and ramet

Priors

- limits based on possible forcing accumulation
- gamma distribution for intercept
- half normal for offset parameter standard deviations



Fit in Stan via brms package

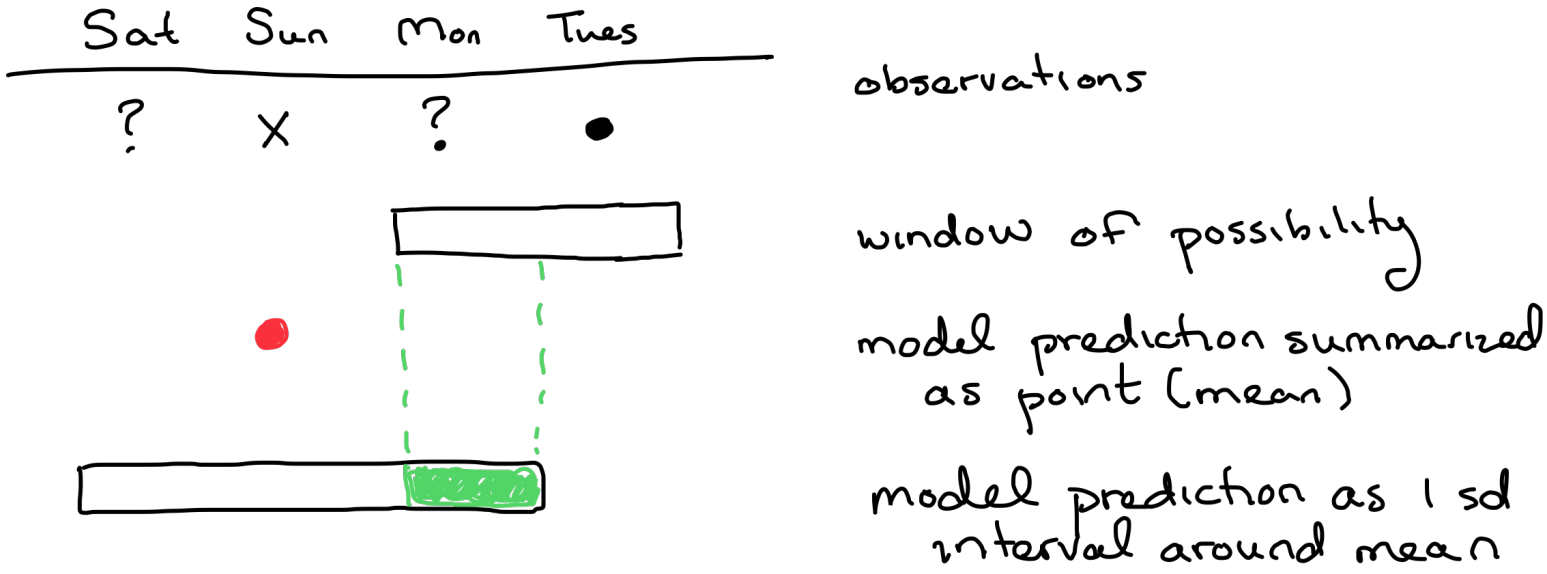
```
# model formula
bform <- brmsformula(sum_forcing | cens(censored, upper) ~
                       MAT + (1|Site) + (1|Clone) + (1|Year) + (1|Tree)

# model prior
bprior <- c(prior("gamma(3.65, 0.01)", class = "Intercept"),
            prior("normal(0,15)", class = "sigma"),
            prior("normal(0,9)", class = "sd"),
            prior("normal(0,5)", class = "b"))

# female/receptivity begin
fbfit <- brm(bform, data = fbdat,
             prior = bprior,
             init = initpars,
             iter = 4000,
             cores = 6,
             chains = 6)
```

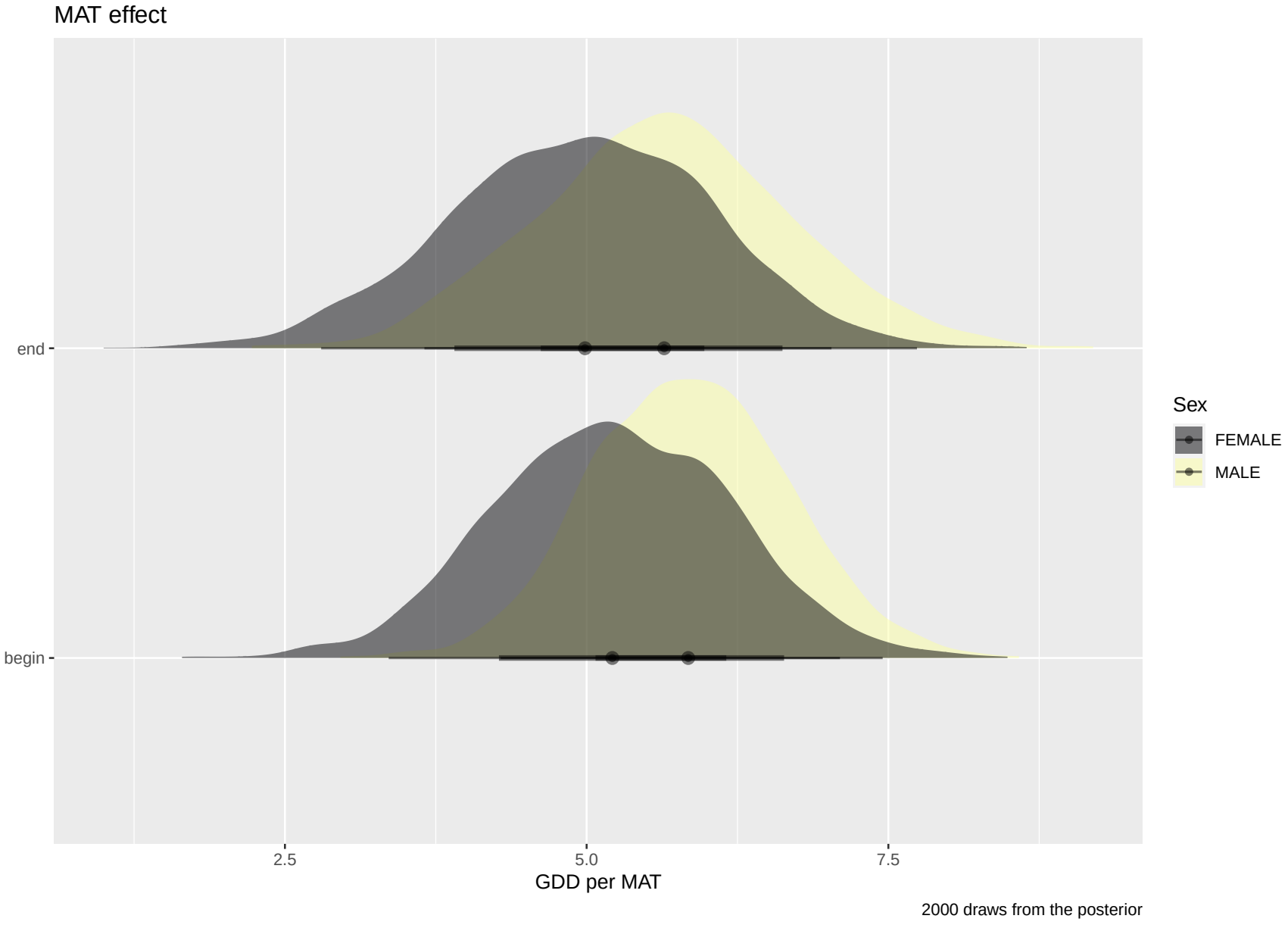
Fit

Modelling events I didn't observe - so how can I check how my model is doing?

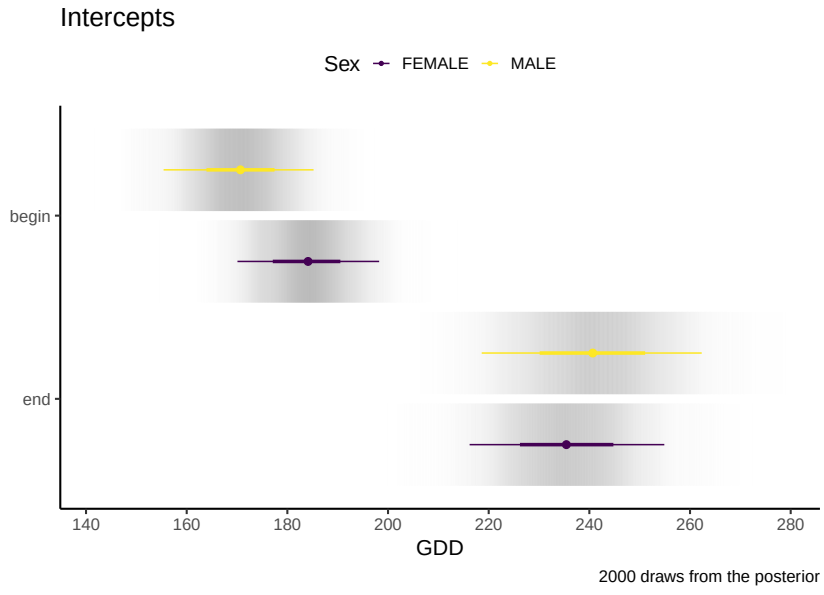


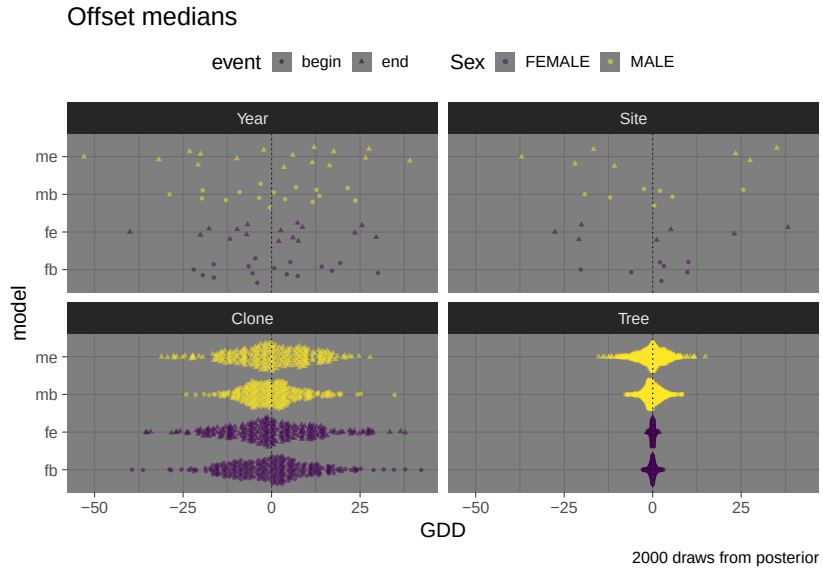
Sex	Begin	Begin_sd	End	End_sd
FEMALE	0.61	0.97	0.71	0.97
MALE	0.76	0.99	0.71	0.97

Results - Provenance effect similar for end and begin

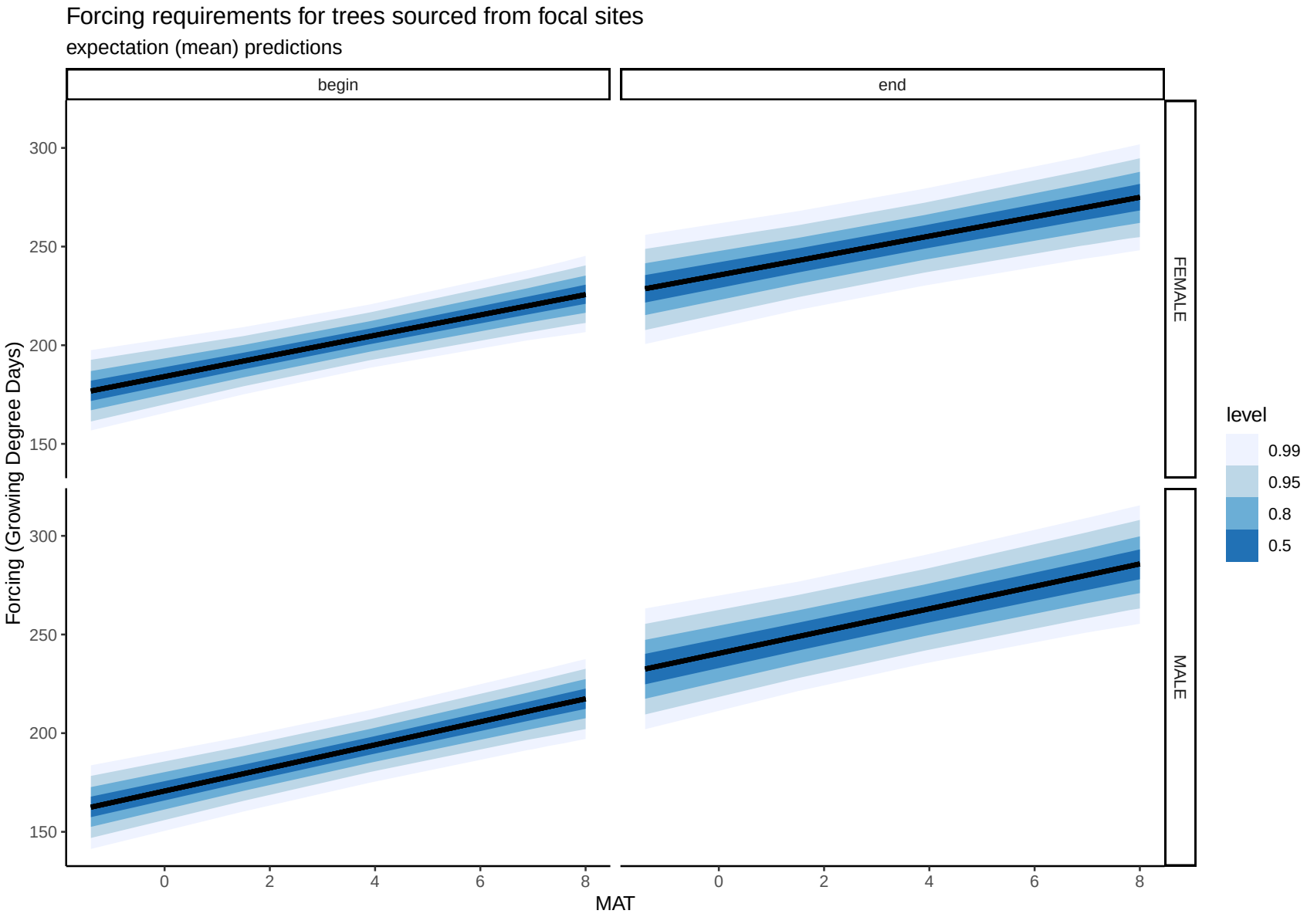


Results - Mean and variation





Results - Forcing predictions expectation



Day of year predictions intro

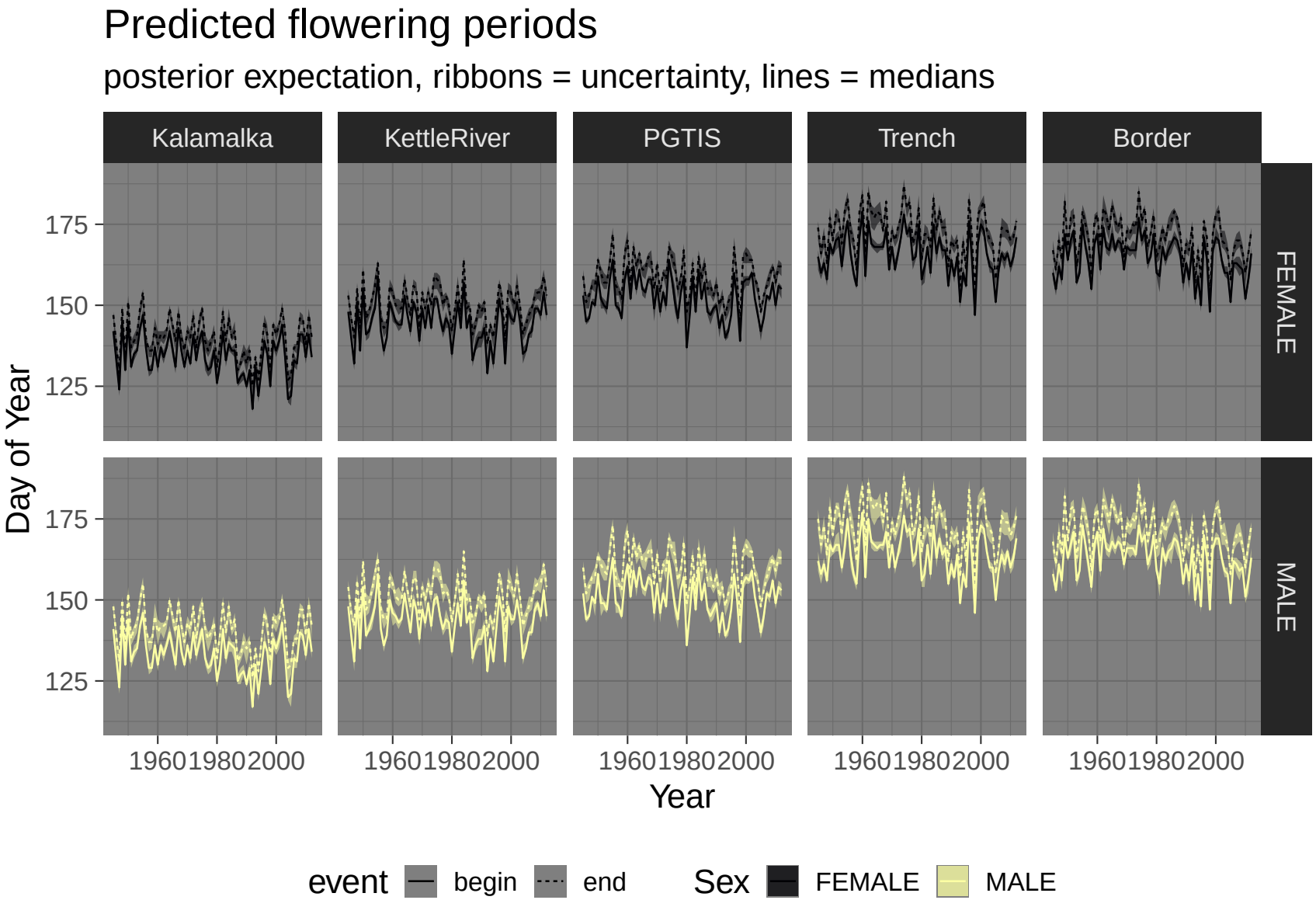
Temperature timeseries -> forcing accumulation timeseries

Then match to forcing predictions

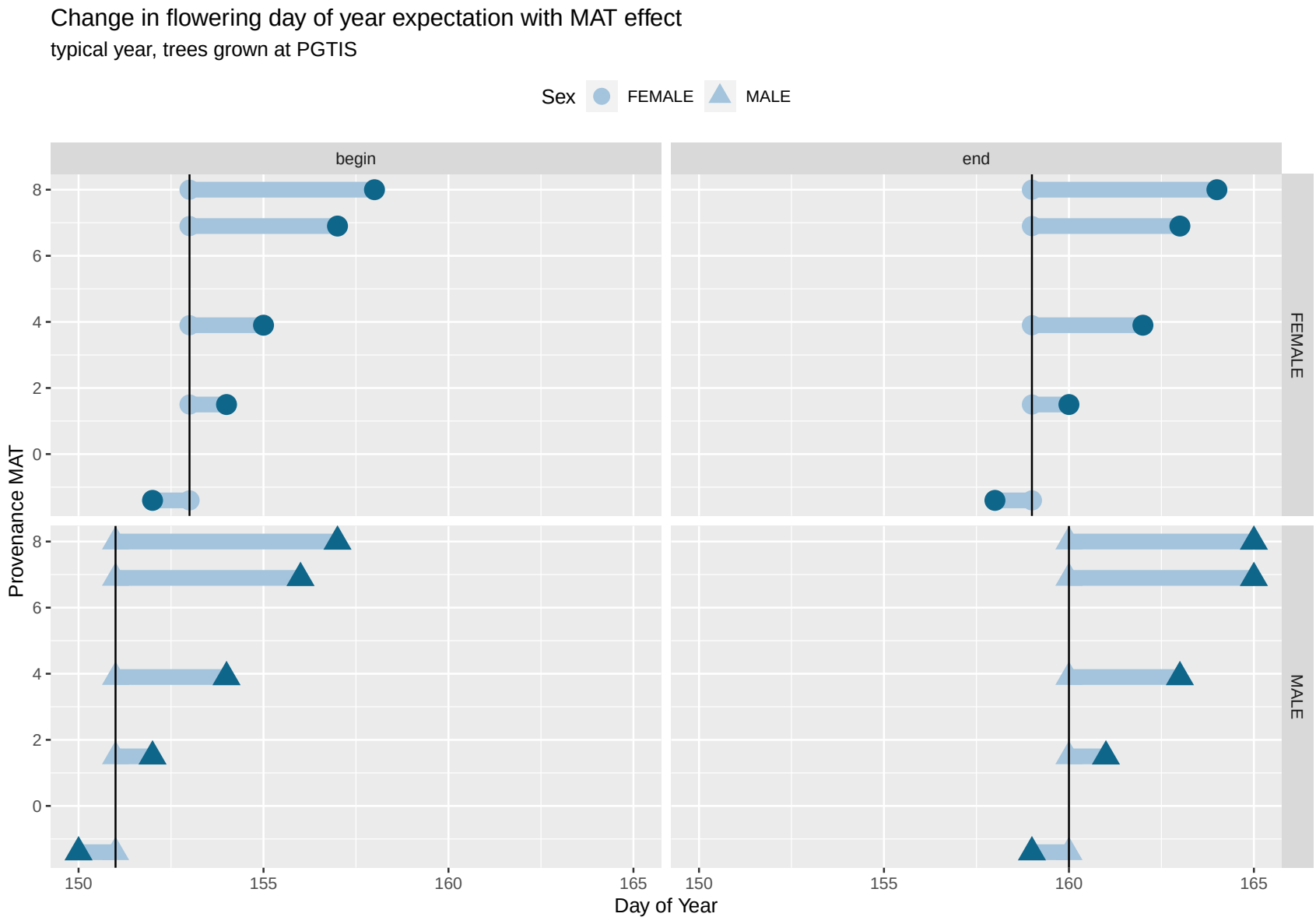
Focus on 5 sites (as provenances as sites)

Site	MAT	Elevation
Border	-1.4	671
Trench	1.5	659
PGTIS	3.9	598
KettleRiver	6.9	632
Kalamalka	8.0	486

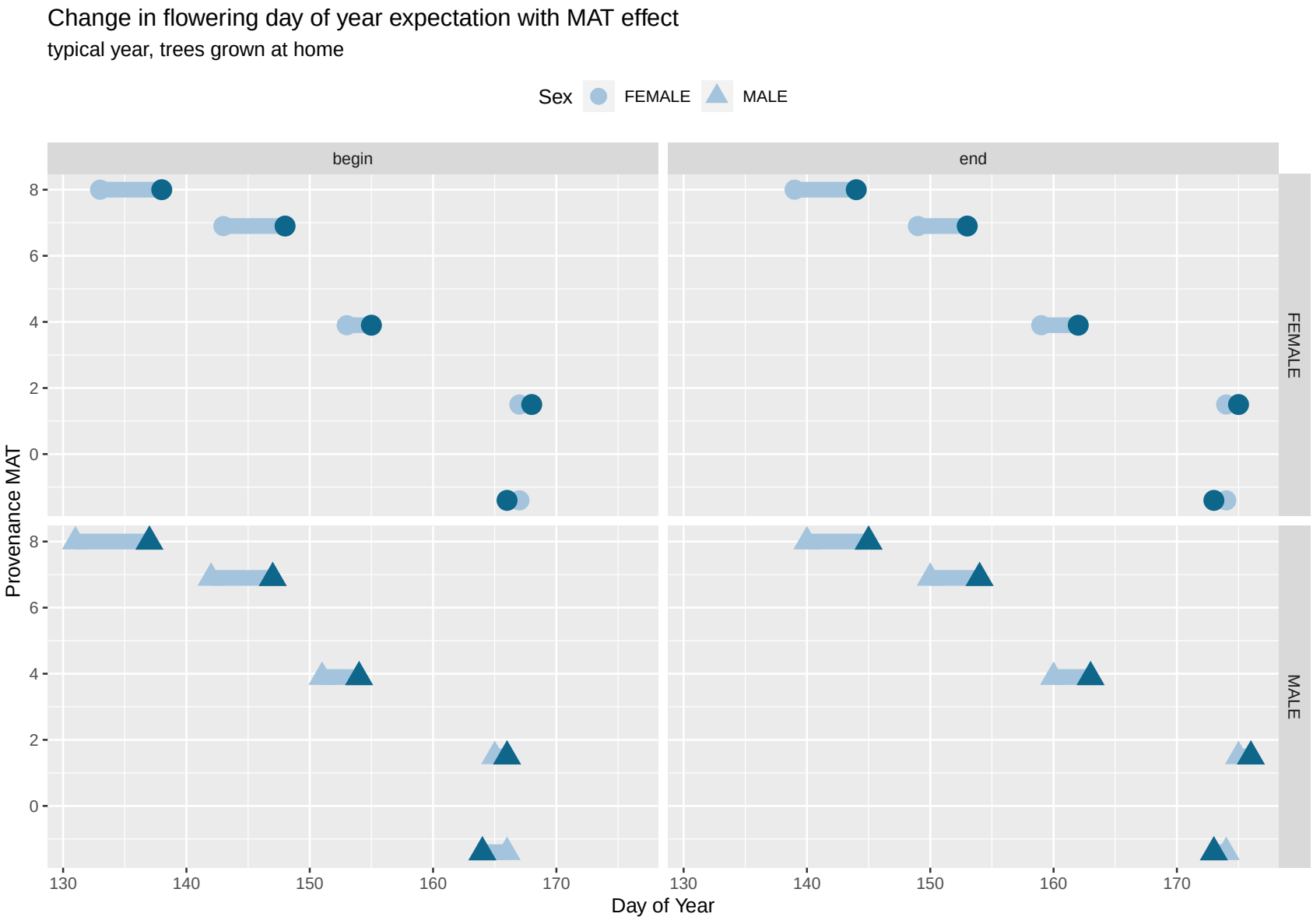
Results - MAT Day of Year



Results - DoY expectations in common garden

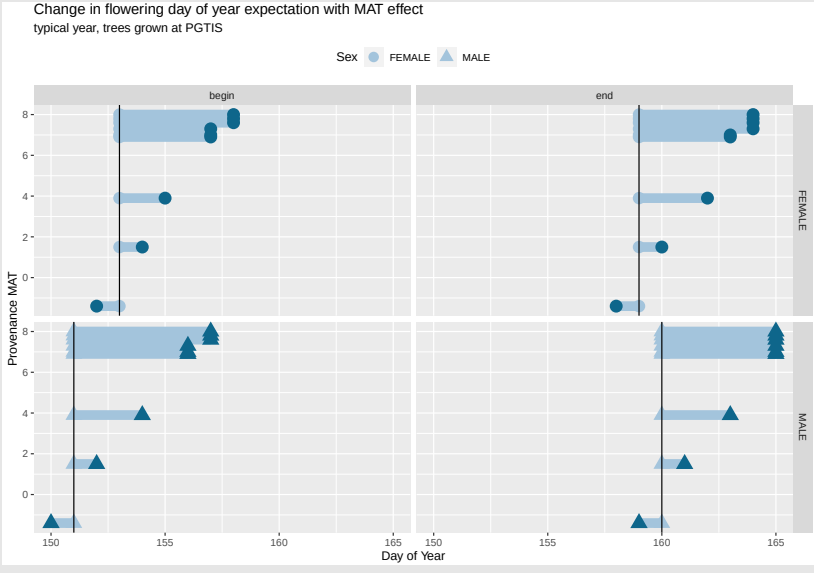


Results - DoY expecations on the landscape

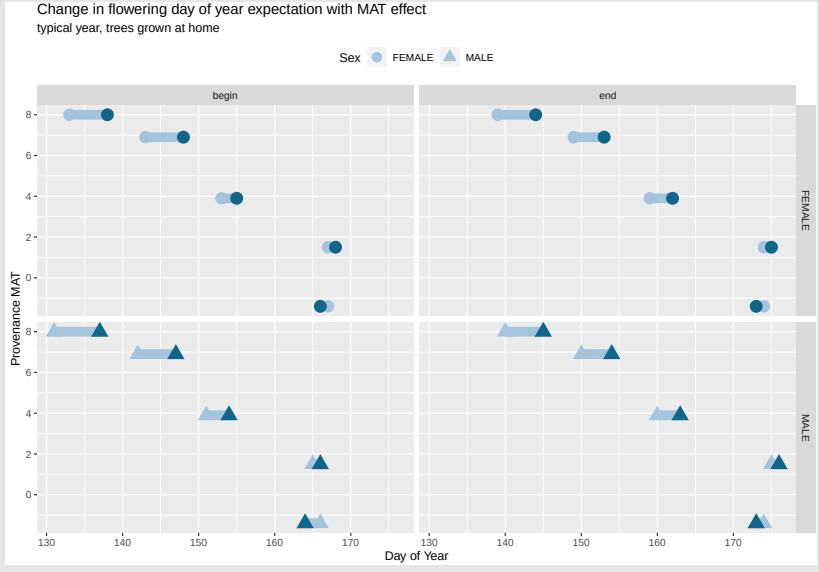


Results - MAT Day of Year

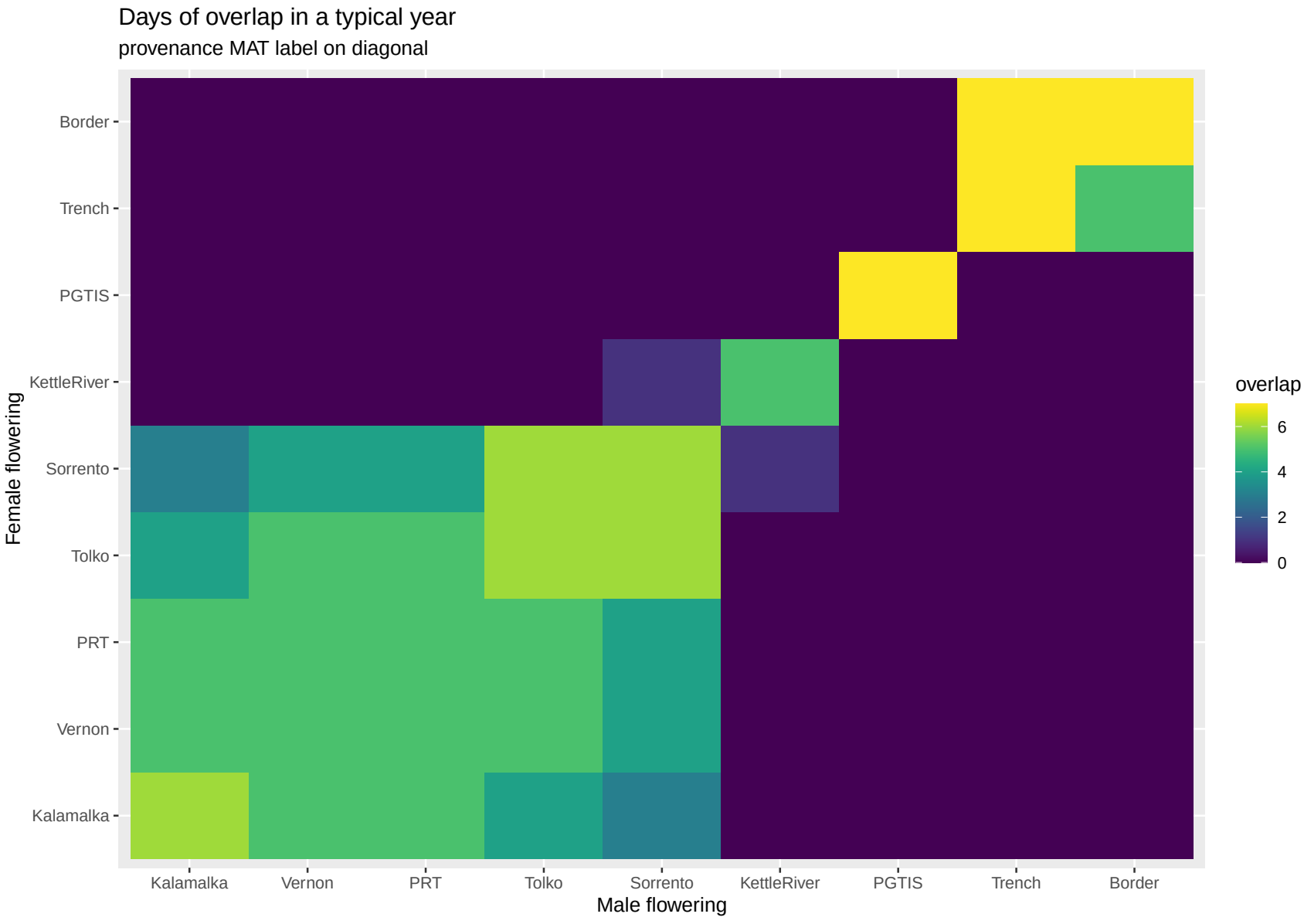
Common garden



Home



Overlap


Days of overlap in a typical year
provenance MAT label on diagonal
Female flowering
Border
Trench
PGTIS
KettleRiver
Sorrento
Tolko
PRT
Vernon
Kalamalka
Kalamalka
Vernon
PRT
Tolko
Sorrento
KettleRiver
PGTIS
Trench
Border
Male flowering
overlap
6
4
2
0

Summary

- Males have longer period and start slightly before, end after females
- ~5 more GDD per 1 degree MAT required for flowering
- Countergradient variation should increase flowering period overlap
- Overlap depends on geographic location and provenance climate

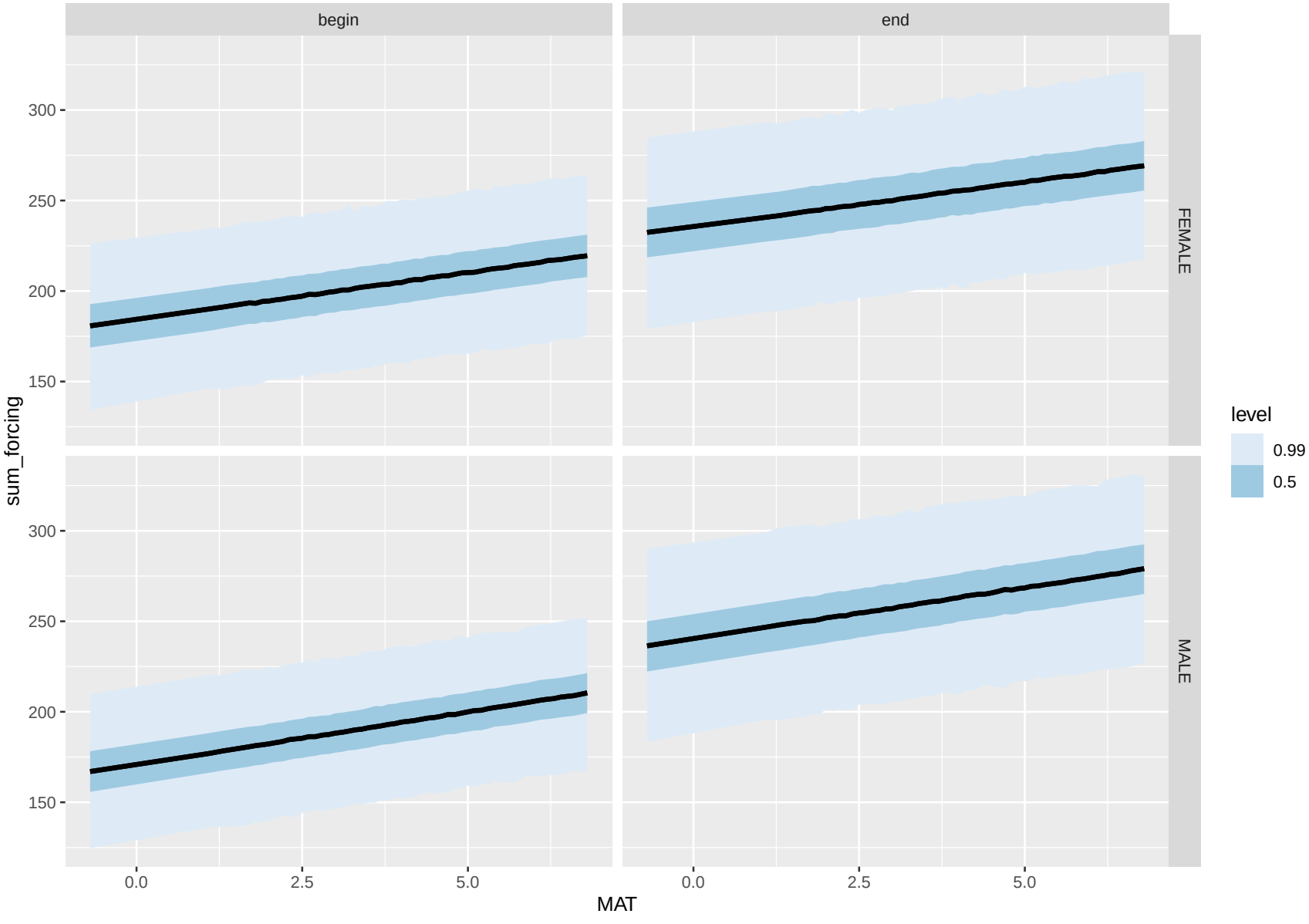
Questions

- But why is there countergradient variation?

More

- Climate change (1 month shift, no big overlap changes)
- Does it all wash away in the light of individual variation?

Extra


begin
end
FEMALE
MALE
sum_forcing
300
250
200
150
0.0
2.5
5.0
MAT
level
0.99
0.5