

1   Forecasting floral futures: leveraging genetic and  
2   microenvironmental data to improve seed  
3   provenancing under climate change

4   Andhika R. Putra<sup>1</sup>, Jian D.L. Yen<sup>2</sup>, Alexandre Fournier-Level<sup>1</sup>

5   <sup>1</sup> School of BioSciences, The University of Melbourne, Parkville, VIC 3010, Australia; <sup>2</sup> Arthur  
6   Rylah Institute for Environmental Research, Heidelberg, VIC 3084, Australia

7   **Author for correspondence:** Alexandre Fournier-Level T: +61 3 8344 7258 E:  
8   [afournier@unimelb.edu.au](mailto:afournier@unimelb.edu.au)

9   **Statement of authorship:** AFL designed the study; ARP performed modelling work and  
10   analysed the results. JDLY and AFL provided feedback and suggestions throughout the project.  
11   ARP wrote the initial draft of the manuscript; all three authors provided edits and revisions.

12   **Data accessibility statement:** Should the manuscript be accepted, we will upload supporting  
13   scripts in a github repository and supporting data in a Figshare repository and include the data  
14   DOI at the end of this article.

15   **Running title:** forecasting floral futures

16   **Keywords:** restoration, revegetation, genomic prediction, functional trait, microclimate,  
17   Arabidopsis thaliana, genetic variation, adaptation

18   **Article type:** Letter

Section	Count
Abstract	142 words
Main Text	5000 words
References	103
Figures	4
Tables	1
Text Boxes	0

# 19 Abstract

20 Revegetation projects seeking to restore degraded ecosystems face a major challenge in  
21 sourcing appropriate plant material, as identifying plants adapted to future climates requires  
22 knowledge of plant performance under novel conditions. In order to support climate-resilient  
23 provenancing efforts, we develop a quantitative trait model that integrates genetic and  
24 microenvironmental variation. We train our model with multiple natural plantings of *Arabidopsis*  
25 *thaliana* and predict days-to-bolting and fecundity across the species' European range. Model  
26 prediction accuracy was high for days-to-bolting and moderate for fecundity, with the majority of  
27 trait variation being explained by temperature variation. Concerningly, fecundity was predicted  
28 to decline under future conditions, although this response was heterogeneous across regions,  
29 and could be offset through the introduction of specific genotypes. Our study highlights the  
30 value of predictive models to aid seed provenancing and improve the success of revegetation  
31 projects.

# 32 Introduction

33 The anthropic perturbation of natural systems continues to be a major threat to biodiversity, with  
34 the modern extinction rate estimated to be up to 100 times higher than the historical average  
35 (Ceballos et al., 2015). A major driver of this biodiversity decline is land-use changes, which  
36 result in the destruction of ecosystems and loss of natural habitat (Tilman et al., 2017). This  
37 problem is compounded by ongoing climate change, which alters remaining habitats to disrupt  
38 local adaptation and produce maladapted genotypes ('genomic offset'; Rellstab et al., 2021).  
39 Indeed, the two processes are inextricably linked in a mutually impactful relationship: land-use  
40 changes both cause and occur in response to climate change (Dale, 1997). Today, recognition  
41 of the damage posed by anthropogenic activities has led to growing interest in developing  
42 methods for restoring degraded ecosystems. This is reflected in the rapid growth of ecological  
43 restoration as a field of research (Wortley et al., 2013) and the increasing amount of resources  
44 spent on restoration projects (Prober et al., 2015).

45

46 A major component of restoration projects is revegetation, which involves the reintroduction of  
47 native plant species into cleared or disturbed areas (Breed et al., 2013) and is essential for  
48 reestablishing complex, self-sufficient ecosystems (Suding et al., 2015). Successful  
49 revegetation hinges on the sourcing of suitable seeds or provenancing (Fedriani et al., 2019)  
50 and was traditionally accomplished by obtaining seeds from nearby populations under the  
51 assumption of local adaptation (Breed et al., 2013). However, the suitability of this approach is  
52 being increasingly challenged because it assumes the long-term persistence of current  
53 environmental conditions (Breed et al., 2013; Broadhurst et al., 2008).

54

55 In reality, the rapid pace of contemporary climate change has clear biological consequences for  
56 plants. These include shifting flowering time (DeLeo et al., 2020; Lu et al., 2006; Primack et al.,  
57 2004; Scheepens & Stöcklin, 2013; Sun et al., 2020), altering root and leaf morphology (Gray &

Brady, 2016; Guerin et al., 2012), and impacting reproductive output (Wheeler et al., 2000; Zhao et al., 2017). Such trait responses to climate change ('climate response') affect overall plant fitness and can lead to uncertainty regarding the long-term success of reintroduced species. Thus, an emerging goal in restoration ecology is to develop strategies for revegetation that account for climate change (Harris et al., 2006; Prober et al., 2015). This includes developing methods to identify and source genetic variation that is pre-adapted to future climates (Ramalho et al., 2017; Supple et al., 2018), such as models predicting climate response under different scenarios.

Climate-responsive fitness traits are often heritable (Bay et al., 2017) and must, by definition, respond adequately to climate variation. These two characteristics indicate that predicting climate response requires accounting for the effects of both genetic and environmental variation. In this regard, quantitative genetics provides a powerful framework for integrating the two sources of variation determining trait values (Daetwyler et al., 2013). Quantitative genetics models can be parameterised with molecular markers to predict traits determined by a few genes (Fournier-Level et al., 2016; Hancock et al., 2011; Seymour et al., 2016; J. Zhang et al., 2016) or with genetic similarity matrices and pedigrees when the genetic architecture is polygenic (Eu-ahsunthornwattana et al., 2014; Gao et al., 2018). Moreover, despite their origin in animal breeding (Wilson et al., 2010) recent developments in quantitative genetics have focused on incorporating environmental variation and genotype-by-environment interactions (GxE) into genomic prediction models (Millet et al., 2019; Montesinos-López et al., 2018; Ramstein et al., 2016; Windhausen et al., 2012).

In this study, we designed a quantitative genetics model to predict quantitative traits in *Arabidopsis thaliana*, a highly diverse annual plant found in Europe, Asia, Africa, and North America (Durvasula et al., 2017; Koornneef & Meinke, 2010). Through the development of a model based on experimental field data, we sought to answer two main questions. Firstly, how

should genetic information be incorporated into predictive models? In plants, common garden experiments have identified moderate- and large-effect quantitative trait loci (QTL) associated with key traits like life history and fitness (Brachi et al., 2010; Gnan et al., 2014; Salomé et al., 2011), which initially suggests a marker-based approach may be suitable. However, QTL may differ across environments (Brachi et al., 2010; Fournier-Level et al., 2011; Linde et al., 2006) due to genotype-by-environment interactions (El-Soda et al., 2014; Sasaki et al., 2015). Across multiple environments, differences in the genomic regions associated with trait variation may lead to a functionally polygenic genetic architecture. If so, we hypothesize that genetic information will be better incorporated via similarity measures than as individual molecular marker effects. Secondly, how should environmental variation be incorporated? Quantitative genetics models are typically environmentally implicit and only consider environmental variation categorically (Montesinos-López et al., 2018; Ramstein et al., 2016; Windhausen et al., 2012). This limits their transferability to the novel conditions relevant for predictive applications. In contrast, a model that allows for continuous environmental variation either through explicit climate predictors or environmental similarity matrices (*sensu* Millet et al., 2019) should be more transferable.

We demonstrate the relevance of our model for ecological restoration by using it to i) predict the spatiotemporal pattern of climate response across *A. thaliana* European range and ii) predict the climate response of known genotypes to various environmental conditions. In doing so, we address two goals that are likely to be relevant for restoration ecology. Firstly, we identified regions of high genomic offset where local plants are predicted to become maladapted in the future and highlighted areas where local provenancing would have been a less suitable strategy for revegetation. Secondly, we identified specific genotypes that could be used in revegetation and demonstrate the value of model predictions for seed sourcing.

# Materials and Methods

## Study Data Set

Two hundred and twenty two genotypes of *A. thaliana* were planted in 4 European field sites scattered over 3 seasons in 2006 and 2007 for a total of 7 plantings (Table S1, Appendix S1), as described in Wilczek et al. (2009, 2014). Across the 7 plantings, 5623 plants were phenotyped for a phenological trait (days-to-bolting, DTB) which marks the transition from vegetative to reproductive phase (Pouteau & Albertini, 2009) and a fitness trait (seed proxy, SP; number of siliques per plant x average length of 5 representative siliques from the plant in mm). All genotypes were present in more than one planting, although no planting contained all genotypes.

The time to bolting is regulated by environmental and genetic factors (Amasino, 2010; Koornneef et al., 1998; Sasaki et al., 2015) and influences reproductive success (Korves et al., 2007), making it a highly relevant climate response trait to model. SP measures reproductive output and was weakly correlated with DTB (Pearson's  $p = 0.058$ ), justifying the construction of separate models for each trait.

## Genetic Variation

Alleles for 10,709,466 biallelic Single Nucleotide Polymorphisms (SNPs) scored across 2029 *Arabidopsis* genotypes were retrieved from publicly available data (Arousse et al., 2020). The genotypes used are inbred lines made homozygous through selfing and single-seed descent, so

allelic states can be coded 0 (homozygous for the reference allele) or 1 (homozygous for the alternative allele) with no heterozygotes. We filtered SNP data to remove SNPs with missing call rate > 0.05 and rare variants with minor allele frequency lower than 0.01. SNPs were then pruned using a window size of 500kb, a variant step count of 100 and a pairwise linkage threshold  $r^2 = 0.1$ , retaining 86,760 SNPs. All filtering and pruning were conducted in PLINK v190b6.10 (Purcell et al., 2007).

Pruned SNPs were used to compute a genetic similarity matrix (GSM; Speed & Balding, 2015). The GSM is a square matrix with entries that measure pairwise similarity between individual genotypes. We compared several methods of constructing GSMs but found they did not affect model performance and that a GSM rendered individual markers redundant as predictors (Appendix S2). Since using a precomputed GSM is more computationally practical than including numerous SNPs for each model run, we decided to only quantify genetic variation through an identity-by-state GSM. Identity-by-state was preferred because it can be computed for any pair of individuals, including novel ones.

## Microclimatic Variation

For each planting, microclimatic conditions were characterized based on the local temperature profile. Temperature is known to be an important environmental cue regulating Arabidopsis development (Granier et al., 2002; Springate & Kover, 2014) and warming is a primary consequence of climate change. On-site ground temperature was initially modelled at hourly resolution for 203 days following field transplantation using daily minimum and maximum temperature (the maximum number of days of data available for all plantings; temperature modeling as described in Wilczek et al., 2010), providing a high-resolution description of temperature conditions. However, lowering the resolution to daily minimum and maximum

temperature yielded equally accurate trait predictions (Appendix S3). We adopted this resolution in our model because this is the typical resolution available for historical records and future projections (Cornes et al., 2018; Gent et al., 2011; Thornton et al., 2016). We used all 203 days of data to describe environmental variation, resulting in 406 (203 x 2) microclimatic predictors.

## Model Description

Genetic and environmental information were combined to construct trait models using a penalized linear-mixed model framework with a LASSO-type penalisation (Tibshirani, 1996) as implemented in the LMM-Lasso package (Rakitsch et al., 2013). Regularization through LASSO-type penalization prevents potential overfitting caused by the large number of predictors. This linear-mixed model takes the form  $y = \Sigma X\beta + \mathbf{u} + \varepsilon$ , where  $y$  is a vector of individual trait values,  $X$  is a matrix of daily minimum and maximum temperature with corresponding fixed effects  $\beta$  (fixed effect),  $\mathbf{u}$  is the random effect of the genetic similarity between pairs of individuals, and  $\varepsilon$  is the vector of residuals, the total number of plants.  $\mathbf{u}$  is unobserved but assumed to be normally distributed with  $\mathbf{u} \sim N(0, \sigma_g^2 \mathbf{K})$ , where  $\mathbf{K}$  is the empirically computed GSM and  $\sigma_g^2$  is the variance explained by the genetic similarity. The residual vector  $\varepsilon$  is also normally distributed  $\varepsilon \sim N(0, \sigma_e^2 \mathbf{I})$ , where  $\mathbf{I}$  is the identity matrix and  $\sigma_e^2$  is the residual variance.

The initial model considered genetic and environmental variation additively and independently ('G+E model'), such that predicted reaction norms across environments were identical for all genotypes. In order to account for the non-linear influence of GxE on climate response, we computed ADMIXTURE proportions (Alexander & Lange, 2011) for each plant using  $k = 4$  ancestral populations, which was found to be optimal (Appendix S4). ADMIXTURE proportions



were used to generate additional predictors  $X_{ADMIXTURE}$ . For  $n$  genotypes and  $r$  microclimatic variables,  $X_{ADMIXTURE}$  is the column-wise Khatri-Rao product  $X_{ADMIXTURE} = (F^T \otimes R^T)^T$ , where  $F$  is the  $n \times k$  matrix of ADMIXTURE proportions and  $R$  is the  $n \times r$  matrix of microclimatic predictors. This produces an  $n \times kr$  matrix of additional predictors whose values are unique for each genotype-environment combination. These predictors were included alongside the minimum and maximum daily temperature (i.e.  $R$ ) in the design matrix  $X'$  to create the 'GxE model' which takes the form  $y = \Sigma X'_j \beta_j + \mathbf{u} + \varepsilon$ .

## Assessing Model Performance

### Internal Validation

Model performance was assessed through a random 10-fold cross validation ('internal validation') with 9 folds of the data used to train the model and the 10<sup>th</sup> fold used to test it. This was repeated 10 times, with each fold acting as the testing set once. Overall model performance was quantified using the root mean square error (RMSE) as a measure of error and the coefficient of determination between observed and predicted values ( $r^2$ ) as a measure of accuracy.

### External Validation

External validation followed an 'environmental blocking' validation strategy (Roberts et al., 2017) designed to assess out-of-sample prediction accuracy. This involved training models on six plantings and testing on the seventh to mimic validation on independent data. Results of environmental blocking were also used to determine the effect of different training set

compositions on model performance.

Finally, we performed an empirical external validation using data from an independent experiment. Korves and colleagues (2007) performed a planting of *A. thaliana* in Rhode Island, USA in Spring 2003 (RS) for which median DTB was reported. RS is geographically (North America vs. Europe) and temporally (2003 vs. 2006-2007) distant from the plantings in our data set, making it a novel environment. We predicted DTB in RS for 77 genotypes using a model trained on 100% of our data and 2 meter air temperature records sourced from DAYMET (Thornton et al., 2016).

## Model Application

The validated model was used to predict broadscale patterns of climate response in *A. thaliana*. This requires inferring the spatial distribution of genetic variation and germination timing on a continental scale. Both components are crucial because they dictate the distribution of plant genotypes and the microclimate they experience, respectively.

## Inferring the spatial distribution of Genetic Variation and Germination Date

We inferred the distribution of *A. thaliana* genetic variation using kriging (Oliver & Webster, 1990), a method of interpolation used in geostatistics for spatially autocorrelated data (Appendix S5). Kriging was considered suitable because spatial autocorrelation in *A. thaliana*'s genetic variation was observed in our dataset (average Moran's  $I=0.146$ ,  $P=0$ ) and is consistent with isolation by distance previously reported in the species (Platt et al., 2010; Sharbel et al., 2000).

We produced a kriged genetic landscape at 1°x1° resolution across Europe by kriging each column of the GSM using the autoKrige function from the automap package (Hiemstra, 2013) in R.

Across its European range, *A. thaliana* germinates at different times of the year (Donohue, 2002). In order to determine the most likely growing season of different sites, we used data from (Exposito-Alonso, 2020) which identified  $k=4$  germination strategies defining coherent climate regions. We smoothed boundaries by replacing the value of outlier cells (those assigned to a different cluster from all its neighbors) with the most common value in the 8 neighboring cells. The four regions (Central Europe CEUR, South Mediterranean SMER, North Mediterranean NMER, Scandinavia SCAN) corresponded to three germination seasons (spring, summer, fall). We assumed all plants germinated on a single date for each season. These dates were February 27 for spring, 25 May for summer, and 3 October for fall and were chosen based on the transplant dates of our plantings.

## Projected Climate Response

We first predicted climate responses across Europe to identify sites that are susceptible to future decline under the RCP2.6 and RCP8.5 climate change scenarios (van Vuuren et al., 2011), with RCP8.5 being a worse scenario. We obtained daily minimum/maximum temperature projections for RCP2.6 from CCSM4 ensemble r1i1p1 (Gent et al., 2011) and for RCP8.5 from CMCC-CM ensemble r1i1p1 (Scoccimarro et al., 2011). Temperature rasters were resampled to 1°x1° to match the resolution of the kriged genetic landscape using the Rraster package (Hijmans et al., 2020).

We predicted DTB and SP from 2041 to 2099 using the RCP projections and in 2006 using temperature records from E-OBS v19.0eHOM (Cornes et al., 2018). We assumed a single

genotype present in each cell (inferred through kriging) and identical germination dates across years. Since bolting occurs before seed production and showed clear boundaries in our data, we restricted predictions of SP to sites where predicted DTB fell within the observed range of 16 to 246 days. We set negative values of SP to zero and converted SP to relative fecundity by dividing by the maximum predicted SP in 2006. This restricted predictions to sites where the model could predict biologically plausible values for both traits and highlighted regions where environmental conditions may fall outside the model capabilities.

Finally, we emulate revegetation attempts by using our model to predict the performance of specific genotypes across Europe under climate change. This allowed us to determine whether known genotypes could be used as a source of “climate-proof” genetic variation at sites where the fitness of local populations was predicted to decline. As a proof-of-concept, we focused on predicting the relative fecundity of the Eden-2 and LI-2 genotypes in 2006 and 2099 under RCP8.5. Eden-2 is a Swedish genotype that must be exposed to prolonged chill before flowering (‘vernalization’, <https://www.arabidopsis.org>), while LI-2 originates from Spain and shows a low expression of the key flowering repressor *FLC* (Rosloski et al., 2013); the two genotypes were predicted to be the latest- and earliest-bolting of the 2029 genotypes, respectively.

# Results

## Internal Validation

Model performance was best when including both genetic and environmental variation, and DTB was overall better-predicted than SP (Table 1). For both traits, the *G only* model predicted a single value for each genotype while the *E only* model predicted a single value for each planting. Regressing predictions from the *G only* and *E only* models against the *G+E* model showed variation in daily minimum/maximum temperature explained more multi-environmental trait variation than genetic differences between individuals (*G+E ~ E only*:  $r^2 = 0.940$  for DTB,  $r^2 = 0.893$  for SP. *G+E ~ G only*:  $r^2 = 0.247$  for DTB,  $r^2 = 0.087$  for SP). This was particularly pronounced for SP, where the *G only* model had a very low  $r^2 = 0.019$ . Accounting for GxE marginally improved model fit for both traits.

**Table 1.** Summary of model performance

Model		RMSE	$r^2$
G only			
	DTB	54.109	0.220
	SN	11446.880	0.019
E only			
	DTB	36.772	0.825
	SN	9618.651	0.391
G+E			
	DTB	20.359	0.889
	SN	8755.630	0.425
GxE			
	DTB	19.074	0.903
	SN	8591.514	0.449

## External Validation

Environmental blocking produced less accurate predictions than those obtained through internal validation (Fig. 1). For DTB, model performance varied greatly depending on which planting was excluded and on the inclusion of GxE. For the *G+E* model, VF and HF had the lowest RMSE (RMSE = 27.928 days and RMSE = 30.648 days respectively), while  $r^2$  was highest for NSP ( $r^2 = 0.497$ ) and NF ( $r^2 = 0.521$ ). DTB was overpredicted in NSU<sup>06</sup> and underpredicted in OF. Including GxE improved predictions for the two summer plantings NSU<sup>06</sup> (RMSE from 46.783 to 10.462 days) and NSU<sup>07</sup> (RMSE from 46.521 to 13.533 days), but offered no improvements in NF and OF. For HF and NSP, DTB was overpredicted such that RMSE increased despite a higher  $r^2$ . For the independent external validation in RS, the *G+E* model had a higher RMSE but higher  $r^2$  (RMSE = 35.574 days,  $r^2 = 0.433$ ) than the GxE model (RMSE = 18.790 days,  $r^2 = 0.097$ ).

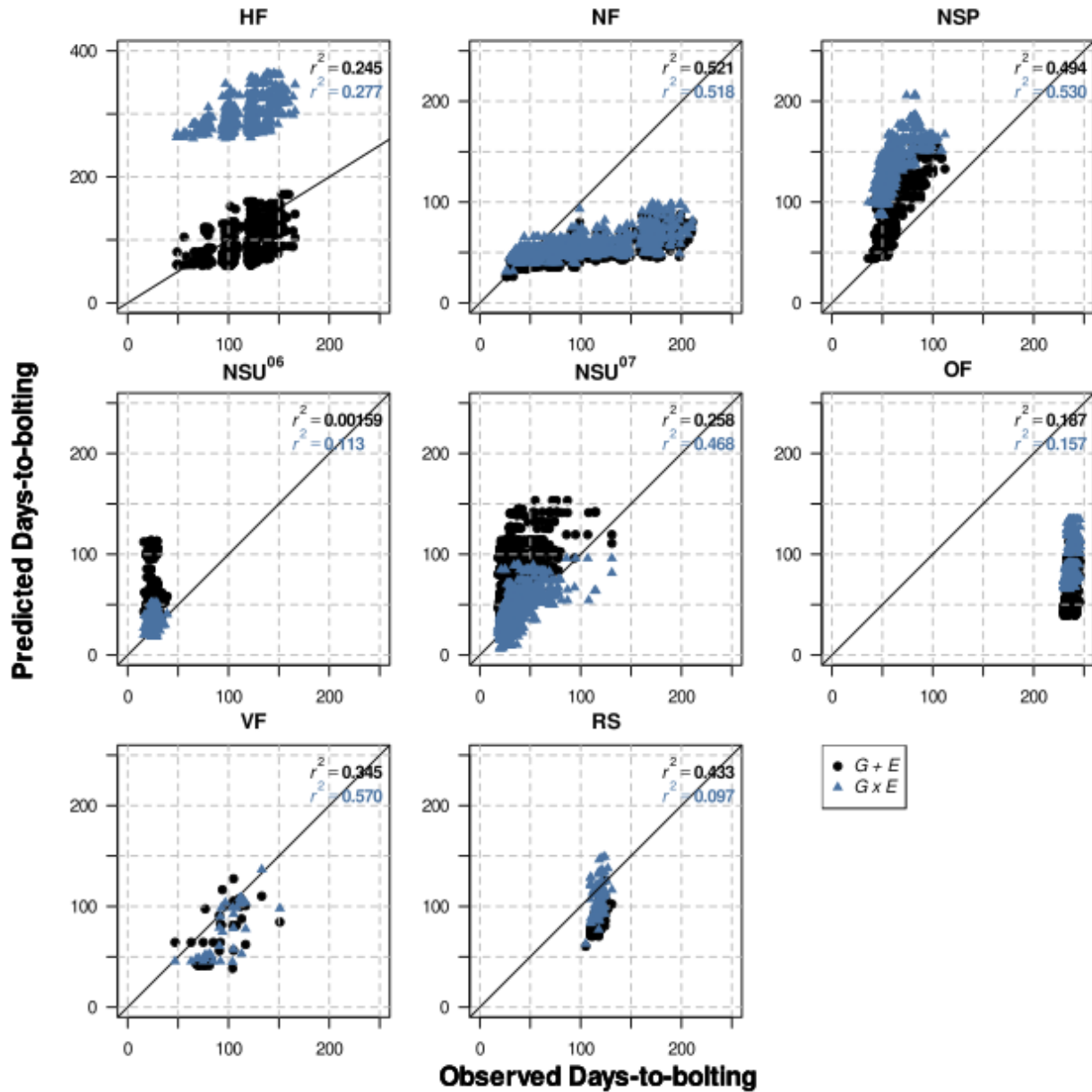


Figure 1: External validation using environmental blocking for days-to-bolting. For all plantings except RS, models were trained on data from six plantings (excluding RS) and validation performed on the seventh planting. For RS, the model was trained on 100% of the data from seven plantings and compared against the median DTB as reported by Korves and colleagues (2007). HF = Halle, Fall 2006. NF = Norwich, Fall 2006. NSP = Norwich, Spring 2007. NSU06 = Norwich, Summer 2006. NSU07 = Norwich, Summer 2007. OF = Oulu, Fall 2007. VF = Valencia, Fall 2006.

Unlike DTB, environmental blocking results for SP did not differ between the two models (Fig. 2). Prediction accuracy was generally poor, with low  $r^2$  for all seven plantings. Interestingly, RMSE was weakly positively correlated with  $r^2$  (Pearson's  $\rho = 0.048$ ). Models were either

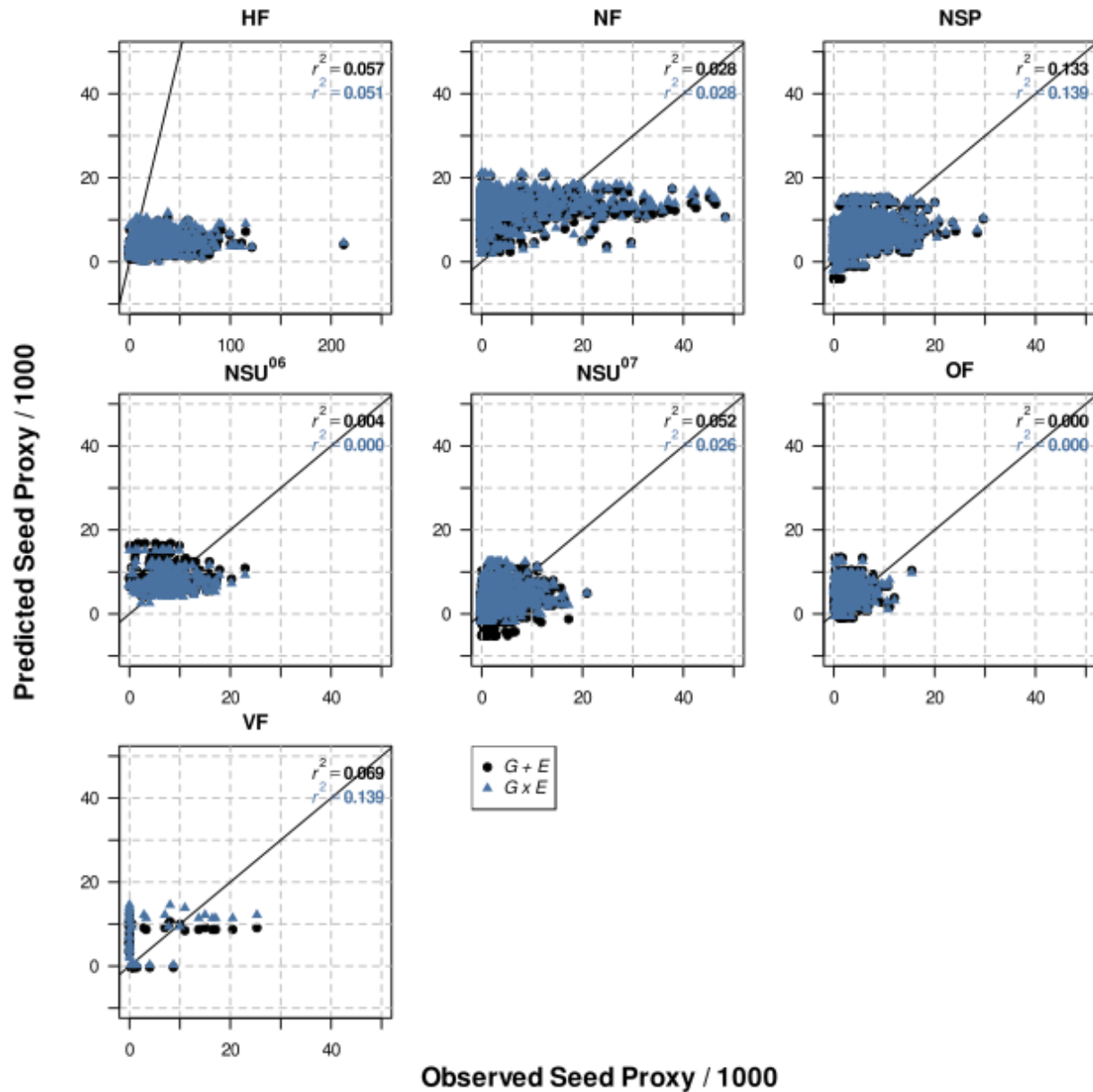
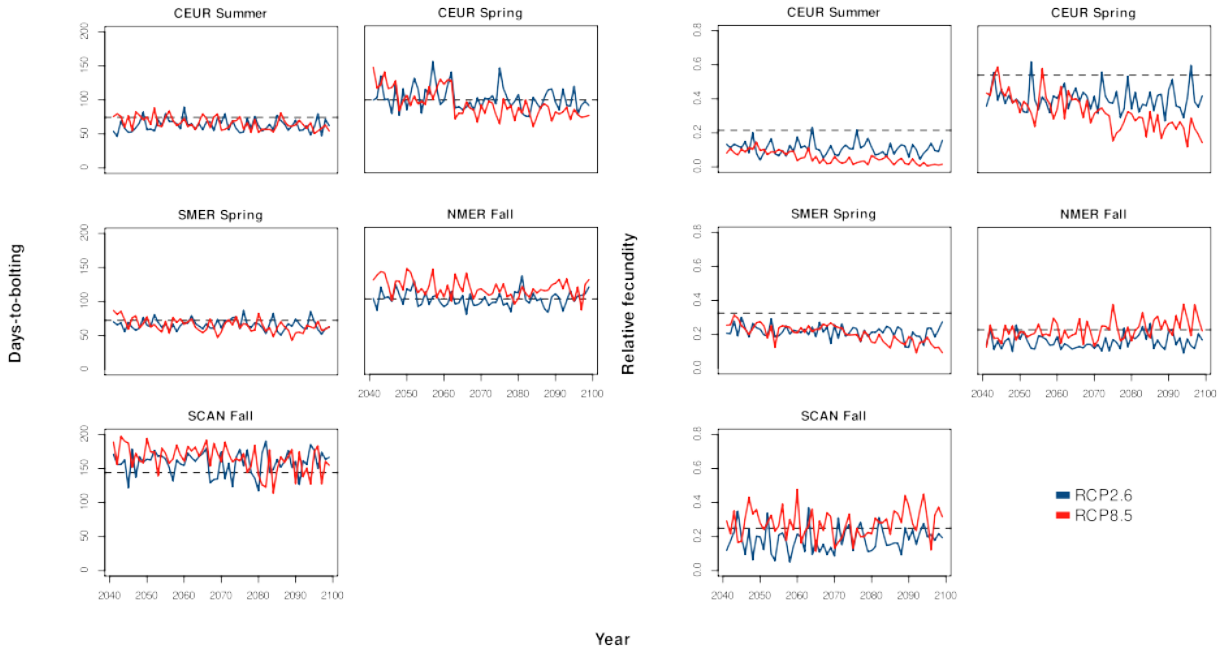


Figure 2: Environmental blocking and external validation results for seed proxy. For all plantings, models were trained on data from six plantings and validation performed on the seventh planting. HF = Halle, Fall 2006. NF = Norwich, Fall 2006. NSP = Norwich, Spring 2007. NSU06 = Norwich, Summer 2006. NSU07 = Norwich, Summer 2007. OF = Oulu, Fall 2007. VF = Valencia, Fall 2006.

predicting SP closer to the observed value or better at ranking different genotypes, but not both.



## 307 Projected Climate Response



*Figure 3: Predicted change in mean days-to-bolting and relative fecundity from 2040 to 2099 for two climate change scenarios. For each region, predictions were created using an ADMIXTURE-based model with  $k = 4$  trained on 100% of the data. At a given location, predicted seed proxy (SP) was set to NA if predicted days-to-bolting fell outside the observed range of 16-246 days and negative values of predicted SP were set to 0. The dashed line indicates the predicted mean of each trait in 2006. Relative fecundity is SP divided by the highest predicted SP in 2006.*

309 The predicted climate response fluctuated annually (Fig. 3) due to the variability of temperature  
 310 projections, although projected conditions all trended towards warming (Fig. S3, Appendix S6).  
 311 Earlier bolting was predicted in CEUR (both cohorts) and SMER, contrasting with the delay in  
 312 bolting predicted for the fall cohorts in SCAN and NMER. Interestingly, the magnitude of this  
 313 delay is lower under RCP8.5 than RCP2.6 in SCAN (mean change in DTB for 2090-2099 under  
 314 RCP8.5  $\Delta DTB_{RCP8.5} = +8$  days, under RCP2.6  $\Delta DTB_{RCP2.6} = +18$  days), whereas the opposite  
 315 was predicted for NMER ( $\Delta DTB_{RCP8.5} = +3$  days,  $\Delta DTB_{RCP2.6} = +1$  day).

316

As for DTB, the predicted change in relative fecundity differed between fall and non-fall cohorts, although this should be interpreted cautiously because SP was much more poorly predicted. Spring and summer cohorts (CEUR, SMER) were predicted to decline in fecundity under both climate change scenario, whereas the mean change in relative fecundity in 2090-2099 is small and near-zero for fall cohorts in SCAN ( $\Delta RF_{RCP8.5} = +0.068$ ,  $\Delta RF_{RCP2.6} = -0.040$ ) and NMER ( $\Delta RF_{RCP8.5} = +0.039$ ,  $\Delta RF_{RCP2.6} = -0.067$ ). Interestingly for SCAN and NMER, fecundity was predicted to increase under the more severe RCP8.5 and decrease under the milder RCP2.6.

We next compared the predicted change in days-to-bolting and relative fecundity for different landscapes of *A. thaliana* genetic variation but strictly comparing 2006 and 2099. Predicted change in days-to-bolting is described in Appendix S7. Here, we focus on predicted change in relative fecundity despite the lower prediction accuracy of SP because its consequence on plant fitness is straightforward to interpret. Under the baseline scenario using the kriged genetic landscape, which assumes the current distribution of genetic variation remains constant, we predicted a decrease in fecundity throughout most of *A. thaliana*'s European range (Figure 4a). Interestingly, the predicted change in fecundity for CEUR differed between the two seasonal cohorts: we predicted increased spring fecundity and decreased summer fecundity in western CEUR, but the opposite in eastern CEUR (Fig. 4a inset).

Finally, we considered a hypothetical revegetation scenario where Eden-2 and LI-2 were introduced throughout Europe. Despite identical environmental conditions, the fecundity response differed dramatically between genotypes (Fig. 4b-c). Eden-2 had higher predicted fecundity than local genotypes in CEUR and SMER – regions where fall germination is expected – but otherwise had lower fecundity than local genotypes. In contrast, LI-2 had higher predicted fecundity than local genotypes throughout most of Europe regardless of the germination season, but was still less fecund than Eden-2 in CEUR and SMER (Fig. 4d).

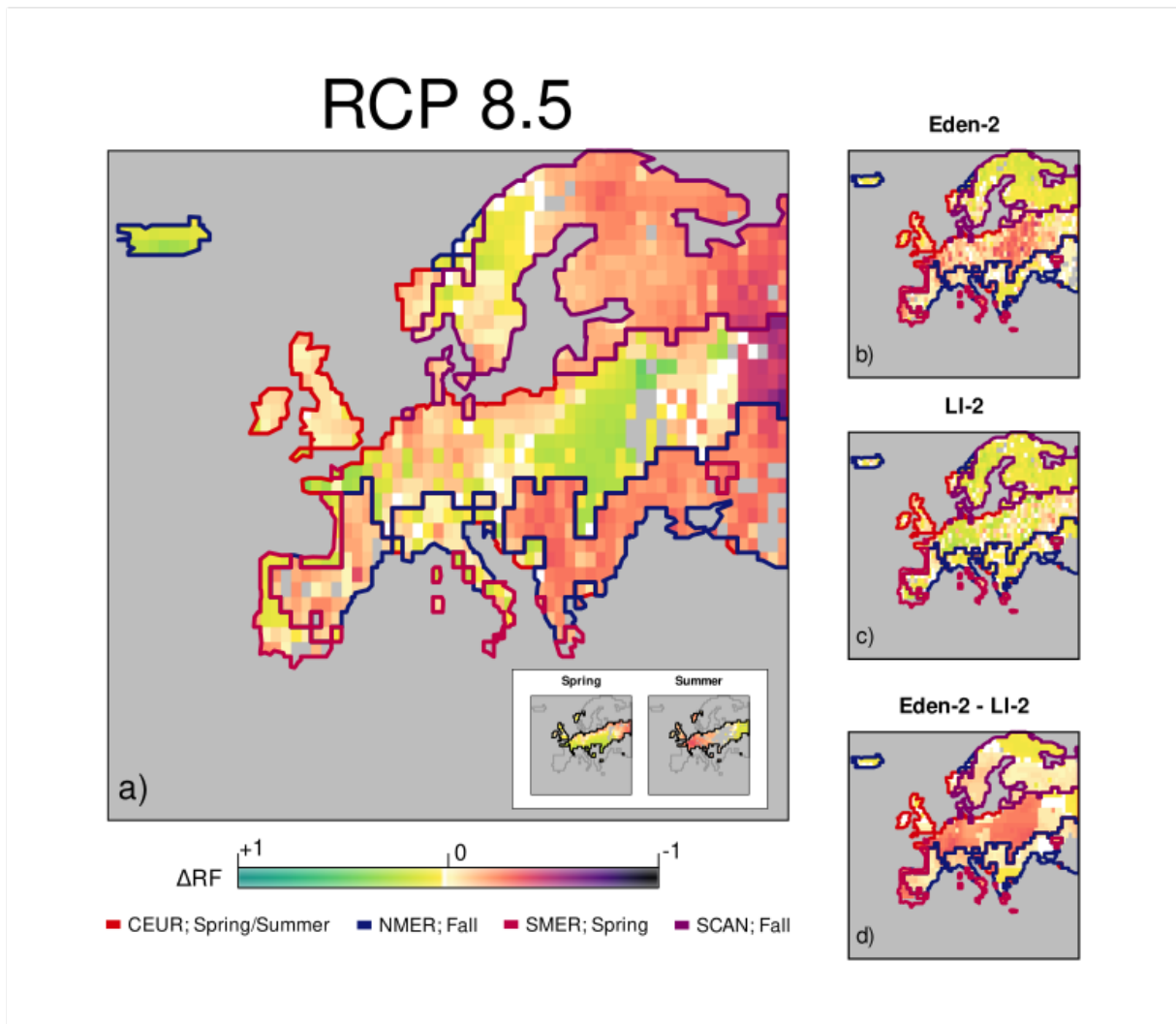


Figure 4: Maps of predicted difference in relative fecundity ( $\Delta RF$ ) across Europe. a) Predicted  $\Delta RF$  in 2099 under RCP8.5 relative to 2006 for the kriged genetic landscape. In CEUR, the predicted  $\Delta RF$  is the mean across the spring and summer cohorts. Inset: predicted  $\Delta RF$  for the spring and summer cohort in CEUR. b) Predicted  $\Delta RF$  across Europe in 2099 and RCP8.5 between Eden-2 and the kriged genetic landscape. c) Predicted  $\Delta RF$  between LI-2 and the kriged genetic landscape. d)  $\Delta RF$  between Eden-2 and LI-2. Cells are colored gray if predicted DTB falls outside the observed range of 16-246 days. Borders indicate the different germination strategy regions. CEUR = Central Europe. NMER = North Mediterranean. SMER = South Mediterranean. SCAN = Scandinavia.

344

345

# Discussion

The interaction between genotype and the environment greatly differed across regions and was shown to be important for predicting plant response to climate change. This can be modelled by including microclimatic predictors in a quantitative trait model, which improves prediction accuracy and allows forecasting the response for different genetic and climate scenarios. For the different scenarios tested in European *A. thaliana*, we predicted heterogeneous climate response depending on both the distribution of genetic variation and spatiotemporal pattern of temperature variation. Our predictions highlighted the complexity of the response to climate change and the breakdown of local adaptation over time that should be accounted for when envisioning ecological restoration.

## Including genetic and environmental variation improves model performance

The inclusion of microclimatic predictors improved model performance relative to genotype-only models for both traits. Genetic variation alone explained only a small proportion of phenotypic variation and could be captured in a GSM. This supports our hypothesis that GxE alters the genetic architecture of traits across environments and renders individual markers uninformative (Brachi et al., 2010; El-Soda et al., 2014; Fournier-Level et al., 2011; Linde et al., 2006). The method used to compute pairwise genetic similarity did not affect model performance (Table S2 & S3, Appendix S2), suggesting they produced functionally identical descriptions of genetic similarity. Eu-ahsunthornwattana and colleagues (2014) also reported high correlation between

different genetic similarity estimates in humans, suggesting that our framework is likely to be broadly applicable.

Phenotypic variation was mainly explained by temperature differences between the plantings. This was expected: climate-responsive traits are by definition affected by environmental conditions, and the influence of temperature on plant phenotypes is well-established (Anderson et al., 2012; Arft et al., 1999; Foden et al., 2007; Schwartz & Hanes, 2010; Sun et al., 2020; Zhao et al., 2017). Our approach distinguishes itself by using microclimatic time series data instead of low-resolution environmental predictors such as the Bioclim variables (Fick & Hijmans, 2017). This functional approach defines conditions as experienced by plants throughout their growing period, rather than through summary climate variables that condense years of weather data into a single statistic. This is necessary because *A. thaliana* plants can occupy the same geographical site but experience very different environments due to variation in germination time (Donohue et al., 2005). Predictors based on monthly, quarterly, or yearly averages cannot account for the multiple seasonal cohorts germinating in a single location. Moreover, long-term averages cannot account for the effects of climate change on temperature variability (Bathiany et al., 2018; Schär et al., 2004; Screen, 2014) and the distinct responses of plants to changes in mean temperature and temperature variability (Burghardt et al., 2016; Scheepens et al., 2018; Wheeler et al., 2000). Experimental studies have typically used a consistent increase in temperature to simulate climate change (Fournier-Level et al., 2016; Li et al., 2014; E. S. Post et al., 2008; Sherry et al., 2007; Springate & Kover, 2014) while maintaining current patterns of variability (Springate & Kover, 2014), but this may not reflect actual patterns of climate change. In comparison, our model considers both the daily range of temperature and temperature variation between days. This may allow predictions to better match trait values of natural populations, which is particularly relevant for restoration projects that will introduce plants to uncontrolled conditions. A tradeoff in our model is the multicollinearity of predictors, which results in non-independent effect sizes that do not lend themselves to biological

interpretation. However, this is less relevant to our primary aim of predicting plant performance for multiple genotypes to identify those suitable for revegetation.

Environmental variation was also an important determinant of model performance in external validation, with predictions being more accurate when the training set contained data from an environment similar to the testing set. For example, VF was well-predicted because the training set contained data from HF and NF. In contrast, DTB in OF was consistently underpredicted because it was unique as Scandinavian and non-Scandinavian falls are functionally distinct environments. *A. thaliana* growing in Scandinavia are reported to be obligate winter cyclers that overwinter under snow cover and flower only in spring (Exposito-Alonso, 2020), whereas those growing further south are facultative winter cyclers that can finish their life cycle before snowfall (Li et al., 2014). Consequently, a model fitted only to data from early-bolting fall cohorts (VF, HF, NF) cannot improve prediction accuracy in OF, where conditions are expected to delay bolting until spring. For the purposes of seed sourcing and revegetation, our findings suggest environmentally diverse data is crucial to maximizing confidence in model predictions. Despite being resource-intensive, the required data may already exist for tree species where provenance testing has been carried out for centuries (Mátyás, 1996).

Although our study was performed in the well-characterized model species *A. thaliana*, we only used generic, easy-to-obtain data and avoided *A. thaliana*-specific biological assumptions to ensure our framework is transferable to non-model species. We computed GSMs using genomic SNPs selected without prior knowledge of their association with DTB or SP and defined environmental conditions using only temperature. In theory, additional predictors known to be biologically relevant could have been included like herbivory, soil nutrient level, and soil microbial composition (Fitzpatrick et al., 2019; Krannitz et al., 1991; Sills & Nienhuis, 1995; Weinig et al., 2003). In practice, doing so would decrease model transferability – the information required to generate predictions in novel conditions becoming harder to obtain as the predictors

become more specific and greater ecophysiological knowledge of the target species is required.

## Predicted climate response and potential applications

We predict temporally and spatially heterogeneous responses to climate change in the coming decades. Despite high interannual variability, the general trends were consistent with previous findings (Cook et al., 2012; Daele et al., 2012; E. Post et al., 2018; Wu et al., 2017; Yu et al., 2010; X. Zhang et al., 2007). In Scandinavia, the predicted delay in DTB likely reflects the disruptive effect of winter warming on vernalization (Cook et al., 2012; Wu et al., 2017; X. Zhang et al., 2007). Delayed flowering would increase the period of vegetative growth, causing a downstream increase in reproductive output (Choe et al., 2001; Daele et al., 2012; Tienderen et al., 1996). Conversely, earlier bolting predicted for spring and summer cohorts in Central Europe and South Mediterranean were consistent with expectations from thermal time models of accelerated development at higher temperatures (Chew et al., 2012; Wilczek et al., 2009). The corresponding decline in fecundity may reflect a shortened period of growth and decreased flower production (Scheepens & Stöcklin, 2013), although this is unclear because accelerated development has also been suggested to increase reproductive output (Cook et al., 2012).

While we could not infer the biological causes underlying our predictions, they clearly show a breakdown of current local adaptation and increase in genetic offset caused by climate change. For the majority of Europe, our predictions suggest local provenancing is less effective in the long-term since fecundity is predicted to decline by 2099. Indeed, we identified a source of genetic variation that could help establish climate-resilient populations of *A. thaliana* from an unexpected origin: Spain. The Spanish genotype LI-2 had higher predicted fecundity than local genotypes throughout most of Europe regardless of growing season, and was potentially suitable for boosting climate resilience in locations as disparate as the Balkans, Finland, and Northwestern Russia. Importantly, our findings are supported by empirical reports that southern

genotypes outperformed local genotypes across Europe (Wilczek et al., 2014) and clearly demonstrates the value of moving beyond local provenancing as a strategy for sourcing seeds.

Even so, our findings should not be taken as an absolute sign of future maladaptation. In this study, we assumed the germination date remained constant between years. In reality, germination timing is another climate-responsive trait that relies on environmental cues (Finch-Savage & Leubner-Metzger, 2006) and would likely vary between years. Germination timing strongly affect fitness, as seen in Central Europe where predictions were seasonally and geographically differentiated (Figure 4a). This suggests the potential for *A. thaliana* to shift germination time in response to climate change, a phenomenon that has been observed in alpine species (Mondoni et al., 2012). If this seasonal shift occurs, *A. thaliana* has the potential to avoid maladaptation and persist in the face of climate change.

## Conclusion

Plant response to climate change in the field is complex and can run contrary to empirical expectations (Parmesan & Hanley, 2015). This complexity has made predicting 'real world' patterns of climate response challenging and is a significant barrier to successful, climate-resilient revegetation. Our work addresses this gap by presenting a straightforward way of incorporating genetic variation, environmental variation, and their interaction into a predictive model. Using *A. thaliana* as an example, we demonstrate the capacity for the model to accurately predict non-linear responses to climate change and its potential use in seed provenancing by determining plant performance over time and space. Although the model was developed using a well-characterized species, our framework shows potential for use in non-model species due to its simple data requirements and minimal biological assumptions.



## 474 Acknowledgements

475 The authors would like to thank Mark Taylor for providing the microclimatic data, Daniel Runcie  
476 for helping clarify the math of the models, Moises Exposito-Alonso for sharing germination time  
477 models and Johanna Schmitt for providing feedback on the manuscript.

# References

- Alexander, D. H., & Lange, K. (2011). Enhancements to the ADMIXTURE algorithm for individual ancestry estimation. *BMC Bioinformatics*, 12(1), 246.  
<https://doi.org/10.1186/1471-2105-12-246>
- Amasino, R. (2010). Seasonal and developmental timing of flowering. *The Plant Journal*, 61(6), 1001–1013. <https://doi.org/10.1111/j.1365-313X.2010.04148.x>
- Anderson, J. T., Inouye, D. W., McKinney, A. M., Colautti, R. I., & Mitchell-Olds, T. (2012). Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. *Proceedings of the Royal Society B: Biological Sciences*, 279(1743), 3843–3852. <https://doi.org/10.1098/rspb.2012.1051>
- Arft, A. M., Walker, M. D., Gurevitch, J., Alatalo, J. M., Bret-Harte, M. S., Dale, M., Diemer, M., Gugerli, F., Henry, G. H. R., Jones, M. H., Hollister, R. D., Jónsdóttir, I. S., Laine, K., Lévesque, E., Marion, G. M., Molau, U., Mølgaard, P., Nordenhäll, U., Raszhivin, V., ... Wookey, P. A. (1999). Responses of Tundra Plants to Experimental Warming:meta-Analysis of the International Tundra Experiment. *Ecological Monographs*, 69(4), 491–511. [https://doi.org/10.1890/0012-9615\(1999\)069\[0491:ROTPTE\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1999)069[0491:ROTPTE]2.0.CO;2)
- Arousse, B., Korte, A., Eeuwijk, F. van, & Kruijer, W. (2020). Imputation of 3 million SNPs in the Arabidopsis regional mapping population. *The Plant Journal*, 102(4), 872–882.  
<https://doi.org/10.1111/tpj.14659>
- Bathiany, S., Dakos, V., Scheffer, M., & Lenton, T. M. (2018). Climate models predict increasing temperature variability in poor countries. *Science Advances*, 4(5), eaar5809.  
<https://doi.org/10.1126/sciadv.aar5809>
- Bay, R. A., Rose, N., Barrett, R., Bernatchez, L., Ghalambor, C. K., Lasky, J. R., Brem, R. B., Palumbi, S. R., & Ralph, P. (2017). Predicting Responses to Contemporary Environmental Change Using Evolutionary Response Architectures. *The American*

- Naturalist*, 189(5), 463–473. <https://doi.org/10.1086/691233>
- Brachi, B., Faure, N., Horton, M., Flahauw, E., Vazquez, A., Nordborg, M., Bergelson, J., Cuguen, J., & Roux, F. (2010). Linkage and Association Mapping of *Arabidopsis thaliana* Flowering Time in Nature. *PLoS Genetics*, 6(5).  
<https://doi.org/10.1371/journal.pgen.1000940>
- Breed, M. F., Stead, M. G., Ottewell, K. M., Gardner, M. G., & Lowe, A. J. (2013). Which provenance and where? Seed sourcing strategies for revegetation in a changing environment. *Conservation Genetics*, 14(1), 1–10. <https://doi.org/10.1007/s10592-012-0425-z>
- Broadhurst, L. M., Lowe, A., Coates, D. J., Cunningham, S. A., McDonald, M., Vesk, P. A., & Yates, C. (2008). Seed supply for broadscale restoration: Maximizing evolutionary potential. *Evolutionary Applications*, 1(4), 587–597. <https://doi.org/10.1111/j.1752-4571.2008.00045.x>
- Burghardt, L. T., Runcie, D. E., Wilczek, A. M., Cooper, M. D., Roe, J. L., Welch, S. M., & Schmitt, J. (2016). Fluctuating, warm temperatures decrease the effect of a key floral repressor on flowering time in *Arabidopsis thaliana*. *New Phytologist*, 210(2), 564–576. <https://doi.org/10.1111/nph.13799>
- Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science Advances*. <https://www.science.org/doi/abs/10.1126/sciadv.1400253>
- Chew, Y. H., Wilczek, A. M., Williams, M., Welch, S. M., Schmitt, J., & Halliday, K. J. (2012). An augmented *Arabidopsis* phenology model reveals seasonal temperature control of flowering time. *New Phytologist*, 194(3), 654–665. <https://doi.org/10.1111/j.1469-8137.2012.04069.x>
- Choe, S., Fujioka, S., Noguchi, T., Takatsuto, S., Yoshida, S., & Feldmann, K. A. (2001). Overexpression of DWARF4 in the brassinosteroid biosynthetic pathway results in increased vegetative growth and seed yield in *Arabidopsis*. *The Plant Journal*, 26(6),

- 573–582. <https://doi.org/10.1046/j.1365-313x.2001.01055.x>
- Cook, B. I., Wolkovich, E. M., & Parmesan, C. (2012). Divergent responses to spring and winter warming drive community level flowering trends. *Proceedings of the National Academy of Sciences of the United States of America*, 109(23), 9000–9005.  
<https://doi.org/10.1073/pnas.1118364109>
- Cornes, R. C., Schrier, G. van der, Besselaar, E. J. M. van den, & Jones, P. D. (2018). An Ensemble Version of the E-OBS Temperature and Precipitation Data Sets. *Journal of Geophysical Research: Atmospheres*, 123(17), 9391–9409.  
<https://doi.org/10.1029/2017JD028200>
- Daele, I. V., Gonzalez, N., Vercauteren, I., Smet, L. de, Inzé, D., Roldán-Ruiz, I., & Vuylsteke, M. (2012). A comparative study of seed yield parameters in *Arabidopsis thaliana* mutants and transgenics. *Plant Biotechnology Journal*, 10(4), 488–500.  
<https://doi.org/10.1111/j.1467-7652.2012.00687.x>
- Daetwyler, H. D., Calus, M. P. L., Pong-Wong, R., Campos, G. de los, & Hickey, J. M. (2013). Genomic Prediction in Animals and Plants: Simulation of Data, Validation, Reporting, and Benchmarking. *Genetics*, 193(2), 347–365.  
<https://doi.org/10.1534/genetics.112.147983>
- Dale, V. H. (1997). The Relationship Between Land-Use Change and Climate Change. *Ecological Applications*, 7(3), 753–769. [https://doi.org/10.1890/1051-0761\(1997\)007\[0753:TRBLUC\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1997)007[0753:TRBLUC]2.0.CO;2)
- DeLeo, V. L., Menge, D. N. L., Hanks, E. M., Juenger, T. E., & Lasky, J. R. (2020). Effects of two centuries of global environmental variation on phenology and physiology of *Arabidopsis thaliana*. *Global Change Biology*, 26(2), 523–538.  
<https://doi.org/10.1111/gcb.14880>
- Donohue, K. (2002). Germination Timing Influences Natural Selection on Life-History Characters in *Arabidopsis Thaliana*. *Ecology*, 83(4), 1006–1016.  
[https://doi.org/10.1890/0012-9658\(2002\)083\[1006:GTINSO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[1006:GTINSO]2.0.CO;2)

- Donohue, K., Dorn, L., Griffith, C., Kim, E., Aguilera, A., Polisetty, C. R., & Schmitt, J. (2005). Niche Construction Through Germination Cueing: Life-History Responses to Timing of Germination in *Arabidopsis thaliana*. *Evolution*, 59(4), 771–785.  
<https://doi.org/10.1111/j.0014-3820.2005.tb01752.x>
- Durvasula, A., Fulgione, A., Gutaker, R. M., Alacakaptan, S. I., Flood, P. J., Neto, C., Tsuchimatsu, T., Burbano, H. A., Picó, F. X., Alonso-Blanco, C., & Hancock, A. M. (2017). African genomes illuminate the early history and transition to selfing in *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences*, 114(20), 5213–5218. <https://doi.org/10.1073/pnas.1616736114>
- El-Soda, M., Malosetti, M., Zwaan, B. J., Koornneef, M., & Aarts, M. G. M. (2014). Genotype × environment interaction QTL mapping in plants: Lessons from *Arabidopsis*. *Trends in Plant Science*, 19(6), 390–398. <https://doi.org/10.1016/j.tplants.2014.01.001>
- Eu-ahsunthornwattana, J., Miller, E. N., Fakiola, M., Jeronimo, S. M. B., Blackwell, J. M., & Cordell, H. J. (2014). Comparison of Methods to Account for Relatedness in Genome-Wide Association Studies with Family-Based Data. *PLoS Genetics*, 10(7). <https://doi.org/10.1371/journal.pgen.1004445>
- Exposito-Alonso, M. (2020). Seasonal timing adaptation across the geographic range of *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences*, 117(18), 9665–9667. <https://doi.org/10.1073/pnas.1921798117>
- Fedriani, J. M., Garrote, P. J., Calvo, G., Delibes, M., Castilla, A. R., & Żywiec, M. (2019). Combined effects of seed provenance, plant facilitation and restoration site on revegetation success. *Journal of Applied Ecology*, 56(4), 996–1006.  
<https://doi.org/10.1111/1365-2664.13343>
- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37(12), 4302–4315.  
<https://doi.org/10.1002/joc.5086>
- Finch-Savage, W. E., & Leubner-Metzger, G. (2006). Seed dormancy and the control of

- germination. *New Phytologist*, 171(3), 501–523. <https://doi.org/10.1111/j.1469-8137.2006.01787.x>
- Fitzpatrick, C. R., Mustafa, Z., & Viliunas, J. (2019). Soil microbes alter plant fitness under competition and drought. *Journal of Evolutionary Biology*, 32(5), 438–450. <https://doi.org/10.1111/jeb.13426>
- Foden, W., Midgley, G. F., Hughes, G., Bond, W. J., Thuiller, W., Hoffman, M. T., Kalemé, P., Underhill, L. G., Rebelo, A., & Hannah, L. (2007). A changing climate is eroding the geographical range of the Namib Desert tree *Aloe* through population declines and dispersal lags. *Diversity and Distributions*, 13(5), 645–653. <https://doi.org/10.1111/j.1472-4642.2007.00391.x>
- Fournier-Level, A., Korte, A., Cooper, M. D., Nordborg, M., Schmitt, J., & Wilczek, A. M. (2011). A Map of Local Adaptation in *Arabidopsis thaliana*. *Science*, 334(6052), 86–89. <https://doi.org/10.1126/science.1209271>
- Fournier-Level, A., Perry, E. O., Wang, J. A., Braun, P. T., Migneault, A., Cooper, M. D., Metcalf, C. J. E., & Schmitt, J. (2016). Predicting the evolutionary dynamics of seasonal adaptation to novel climates in *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences*, 113(20), E2812–E2821. <https://doi.org/10.1073/pnas.1517456113>
- Gao, N., Teng, J., Ye, S., Yuan, X., Huang, S., Zhang, H., Zhang, X., Li, J., & Zhang, Z. (2018). Genomic Prediction of Complex Phenotypes Using Genic Similarity Based Relatedness Matrix. *Frontiers in Genetics*, 9. <https://doi.org/10.3389/fgene.2018.00364>
- Gent, P. R., Danabasoglu, G., Donner, L. J., Holland, M. M., Hunke, E. C., Jayne, S. R., Lawrence, D. M., Neale, R. B., Rasch, P. J., Vertenstein, M., Worley, P. H., Yang, Z.-L., & Zhang, M. (2011). The Community Climate System Model Version 4. *Journal of Climate*, 24(19), 4973–4991. <https://doi.org/10.1175/2011JCLI4083.1>
- Gnan, S., Priest, A., & Kover, P. X. (2014). The Genetic Basis of Natural Variation in Seed Size and Seed Number and Their Trade-Off Using *Arabidopsis thaliana* MAGIC Lines.

- Genetics*, 198(4), 1751–1758. <https://doi.org/10.1534/genetics.114.170746>
- Granier, C., Massonnet, C., Turc, O., Muller, B., Chenu, K., & Tardieu, F. (2002). Individual leaf development in *Arabidopsis thaliana*: A stable thermal-time-based programme. *Annals of Botany*, 89(5), 595–604. <https://doi.org/10.1093/aob/mcf085>
- Gray, S. B., & Brady, S. M. (2016). Plant developmental responses to climate change. *Developmental Biology*, 419(1), 64–77. <https://doi.org/10.1016/j.ydbio.2016.07.023>
- Guerin, G. R., Wen, H., & Lowe, A. J. (2012). Leaf morphology shift linked to climate change. *Biology Letters*, 8(5), 882–886. <https://doi.org/10.1098/rsbl.2012.0458>
- Hancock, A. M., Brachi, B., Faure, N., Horton, M. W., Jarymowycz, L. B., Sperone, F. G., Toomajian, C., Roux, F., & Bergelson, J. (2011). Adaptation to Climate Across the *Arabidopsis thaliana* Genome. *Science*, 334(6052), 83–86. <https://doi.org/10.1126/science.1209244>
- Harris, J. A., Hobbs, R. J., Higgs, E., & Aronson, J. (2006). Ecological Restoration and Global Climate Change. *Restoration Ecology*, 14(2), 170–176. <https://doi.org/10.1111/j.1526-100X.2006.00136.x>
- Hiemstra, P. (2013). *automap: Automatic interpolation package* (1.0-14) [Computer software]. <https://CRAN.R-project.org/package=automap>
- Hijmans, R. J., Etten, J. van, Sumner, M., Cheng, J., Baston, D., Bevan, A., Bivand, R., Busetto, L., Canty, M., Forrest, D., Ghosh, A., Golicher, D., Gray, J., Greenberg, J. A., Hiemstra, P., Hingee, K., Geosciences, I. for M. A., Karney, C., Mattiuzzi, M., ... Wueest, R. (2020). *raster: Geographic Data Analysis and Modeling* (3.3-13) [Computer software]. <https://CRAN.R-project.org/package=raster>
- Koornneef, M., Alonso-Blanco, C., Peeters, A. J. M., & Soppe, W. (1998). Genetic control of flowering time in *Arabidopsis*. *Annual Review of Plant Physiology and Plant Molecular Biology*, 49(1), 345–370. <https://doi.org/10.1146/annurev.arplant.49.1.345>
- Koornneef, M., & Meinke, D. (2010). The development of *Arabidopsis* as a model plant. *The Plant Journal*, 61(6), 909–921. <https://doi.org/10.1111/j.1365-313X.2009.04086.x>

- Korves, T. M., Schmid, K. J., Caicedo, A. L., Mays, C., Stinchcombe, J. R., Purugganan, M. D., & Schmitt, J. (2007). Fitness effects associated with the major flowering time gene *FRIGIDA* in *Arabidopsis thaliana* in the field. *The American Naturalist*, 169(5), E141-157. <https://doi.org/10.1086/513111>
- Krannitz, P. G., Aarssen, L. W., & Dow, J. M. (1991). The Effect of Genetically Based Differences in Seed Size on Seedling Survival in *Arabidopsis thaliana* (Brassicaceae). *American Journal of Botany*, 78(3), 446–450. JSTOR. <https://doi.org/10.2307/2444967>
- Li, Y., Cheng, R., Spokas, K. A., Palmer, A. A., & Borevitz, J. O. (2014). Genetic variation for life history sensitivity to seasonal warming in *Arabidopsis thaliana*. *Genetics*, 196(2), 569–577. <https://doi.org/10.1534/genetics.113.157628>
- Linde, M., Hattendorf, A., Kaufmann, H., & Debener, Th. (2006). Powdery mildew resistance in roses: QTL mapping in different environments using selective genotyping. *Theoretical and Applied Genetics*, 113(6), 1081–1092. <https://doi.org/10.1007/s00122-006-0367-2>
- Lu, P., Yu, Q., Liu, J., & Lee, X. (2006). Advance of tree-flowering dates in response to urban climate change. *Agricultural and Forest Meteorology*, 138(1), 120–131. <https://doi.org/10.1016/j.agrformet.2006.04.002>
- Mátyás, C. (1996). Climatic adaptation of trees: Rediscovering provenance tests. *Euphytica*, 92(1), 45–54. <https://doi.org/10.1007/BF00022827>
- Millet, E. J., Kruijer, W., Coupel-Ledru, A., Alvarez Prado, S., Cabrera-Bosquet, L., Lacube, S., Charcosset, A., Welcker, C., van Eeuwijk, F., & Tardieu, F. (2019). Genomic prediction of maize yield across European environmental conditions. *Nature Genetics*, 51(6), 952–956. <https://doi.org/10.1038/s41588-019-0414-y>
- Montesinos-López, A., Montesinos-López, O. A., Gianola, D., Crossa, J., & Hernández-Suárez, C. M. (2018). Multi-environment Genomic Prediction of Plant Traits Using Deep Learners With Dense Architecture. *G3: Genes, Genomes, Genetics*, 8(12), 3813–3828. <https://doi.org/10.1534/g3.118.200740>
- Oliver, M. A., & Webster, R. (1990). Kriging: A method of interpolation for geographical



- information systems. *International Journal of Geographical Information Systems*, 4(3), 313–332. <https://doi.org/10.1080/02693799008941549>
- Parmesan, C., & Hanley, M. E. (2015). Plants and climate change: Complexities and surprises. *Annals of Botany*, 116(6), 849–864. <https://doi.org/10.1093/aob/mcv169>
- Platt, A., Horton, M., Huang, Y. S., Li, Y., Anastasio, A. E., Mulyati, N. W., Ågren, J., Bossdorf, O., Byers, D., Donohue, K., Dunning, M., Holub, E. B., Hudson, A., Corre, V. L., Loudet, O., Roux, F., Warthmann, N., Weigel, D., Rivero, L., ... Borevitz, J. O. (2010). The Scale of Population Structure in *Arabidopsis thaliana*. *PLOS Genetics*, 6(2), e1000843. <https://doi.org/10.1371/journal.pgen.1000843>
- Post, E. S., Pedersen, C., Wilmers, C. C., & Forchhammer, M. C. (2008). Phenological Sequences Reveal Aggregate Life History Response to Climatic Warming. *Ecology*, 89(2), 363–370. <https://doi.org/10.1890/06-2138.1>
- Post, E., Steinman, B. A., & Mann, M. E. (2018). Acceleration of phenological advance and warming with latitude over the past century. *Scientific Reports*, 8(1), 3927. <https://doi.org/10.1038/s41598-018-22258-0>
- Pouteau, S., & Albertini, C. (2009). The significance of bolting and floral transitions as indicators of reproductive phase change in *Arabidopsis*. *Journal of Experimental Botany*, 60(12), 3367–3377. <https://doi.org/10.1093/jxb/erp173>
- Primack, D., Imbres, C., Primack, R. B., Miller-Rushing, A. J., & Tredici, P. D. (2004). Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. *American Journal of Botany*, 91(8), 1260–1264. <https://doi.org/10.3732/ajb.91.8.1260>
- Prober, S., Byrne, M., McLean, E., Steane, D., Potts, B., Vaillancourt, R., & Stock, W. (2015). Climate-adjusted provenancing: A strategy for climate-resilient ecological restoration. *Frontiers in Ecology and Evolution*, 3, 65. <https://doi.org/10.3389/fevo.2015.00065>
- Purcell, S., Neale, B., Todd-Brown, K., Thomas, L., Ferreira, M. A. R., Bender, D., Maller, J., Sklar, P., de Bakker, P. I. W., Daly, M. J., & Sham, P. C. (2007). PLINK: A Tool Set for Whole-Genome Association and Population-Based Linkage Analyses. *American Journal*

- of Human Genetics*, 81(3), 559–575.
- Rakitsch, B., Lippert, C., Stegle, O., & Borgwardt, K. (2013). A Lasso multi-marker mixed model for association mapping with population structure correction. *Bioinformatics*, 29(2), 206–214. <https://doi.org/10.1093/bioinformatics/bts669>
- Ramvalho, C. E., Byrne, M., & Yates, C. J. (2017). A Climate-Oriented Approach to Support Decision-Making for Seed Provenance in Ecological Restoration. *Frontiers in Ecology and Evolution*, 5, 95. <https://doi.org/10.3389/fevo.2017.00095>
- Ramstein, G. P., Evans, J., Kaeppler, S. M., Mitchell, R. B., Vogel, K. P., Buell, C. R., & Casler, M. D. (2016). Accuracy of Genomic Prediction in Switchgrass (*Panicum virgatum* L.) Improved by Accounting for Linkage Disequilibrium. *G3: Genes, Genomes, Genetics*, 6(4), 1049–1062. <https://doi.org/10.1534/g3.115.024950>
- Rellstab, C., Dauphin, B., & Exposito-Alonso, M. (2021). Prospects and limitations of genomic offset in conservation management. *Evolutionary Applications*, 14(5), 1202–1212. <https://doi.org/10.1111/eva.13205>
- Roberts, D. R., Bahn, V., Ciuti, S., Boyce, M. S., Elith, J., Guillera-Arroita, G., Hauenstein, S., Lahoz-Monfort, J. J., Schröder, B., Thuiller, W., Warton, D. I., Wintle, B. A., Hartig, F., & Dormann, C. F. (2017). Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography*, 40(8), 913–929. <https://doi.org/10.1111/ecog.02881>
- Rosloski, S. M., Singh, A., Jali, S. S., Balasubramanian, S., Weigel, D., & Grbic, V. (2013). Functional analysis of splice variant expression of MADS AFFECTING FLOWERING 2 of *Arabidopsis thaliana*. *Plant Molecular Biology*, 81(1–2), 57–69. <https://doi.org/10.1007/s11103-012-9982-2>
- Salomé, P. A., Bomblies, K., Laitinen, R. A. E., Yant, L., Mott, R., & Weigel, D. (2011). Genetic Architecture of Flowering-Time Variation in *Arabidopsis thaliana*. *Genetics*, 188(2), 421–433. <https://doi.org/10.1534/genetics.111.126607>
- Sasaki, E., Zhang, P., Atwell, S., Meng, D., & Nordborg, M. (2015). “Missing” GxE Variation

- Controls Flowering Time in *Arabidopsis thaliana*. *PLOS Genetics*, 11(10), e1005597.  
<https://doi.org/10.1371/journal.pgen.1005597>
- Schär, C., Vidale, P. L., Lüthi, D., Frei, C., Häberli, C., Liniger, M. A., & Appenzeller, C. (2004).  
 The role of increasing temperature variability in European summer heatwaves. *Nature*,  
 427(6972), 332–336. <https://doi.org/10.1038/nature02300>
- Scheepens, J. F., Deng, Y., & Bosssdorf, O. (2018). Phenotypic plasticity in response to  
 temperature fluctuations is genetically variable, and relates to climatic variability of  
 origin, in *Arabidopsis thaliana*. *AoB PLANTS*, 10(4).  
<https://doi.org/10.1093/aobpla/ply043>
- Scheepens, J. F., & Stöcklin, J. (2013). Flowering phenology and reproductive fitness along a  
 mountain slope: Maladaptive responses to transplantation to a warmer climate in  
*Campanula thyrsoidea*. *Oecologia*, 171(3), 679–691. <https://doi.org/10.1007/s00442-012-2582-7>
- Schwartz, M. D., & Hanes, J. M. (2010). Continental-scale phenology: Warming and chilling.  
*International Journal of Climatology*, 30(11), 1595–1598. <https://doi.org/10.1002/joc.2014>
- Scoccimarro, E., Gualdi, S., Bellucci, A., Sanna, A., Giuseppe Fogli, P., Manzini, E., Vichi, M.,  
 Oddo, P., & Navarra, A. (2011). Effects of Tropical Cyclones on Ocean Heat Transport in  
 a High-Resolution Coupled General Circulation Model. *Journal of Climate*, 24(16), 4368–  
 4384. <https://doi.org/10.1175/2011JCLI4104.1>
- Screen, J. A. (2014). Arctic amplification decreases temperature variance in northern mid- to  
 high-latitudes. *Nature Climate Change*, 4(7), 577–582.  
<https://doi.org/10.1038/nclimate2268>
- Seymour, D. K., Chae, E., Grimm, D. G., Pizarro, C. M., Habring-Müller, A., Vasseur, F.,  
 Rakitsch, B., Borgwardt, K. M., Koenig, D., & Weigel, D. (2016). Genetic architecture of  
 nonadditive inheritance in *Arabidopsis thaliana* hybrids. *Proceedings of the National  
 Academy of Sciences*. <https://doi.org/10.1073/pnas.1615268113>
- Sharbel, T. F., Haubold, B., & Mitchell-Olds, T. (2000). Genetic isolation by distance in

- Arabidopsis thaliana*: Biogeography and postglacial colonization of Europe. *Molecular Ecology*, 9(12), 2109–2118. <https://doi.org/10.1046/j.1365-294x.2000.01122.x>
- Sherry, R. A., Zhou, X., Gu, S., Arnone, J. A., Schimel, D. S., Verburg, P. S., Wallace, L. L., & Luo, Y. (2007). Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences*, 104(1), 198–202. <https://doi.org/10.1073/pnas.0605642104>
- Sills, G. R., & Nienhuis, J. (1995). Maternal phenotypic effects due to soil nutrient levels and sink removal in *Arabidopsis thaliana* (Brassicaceae). *American Journal of Botany*, 82(4), 491–495. <https://doi.org/10.1002/j.1537-2197.1995.tb15669.x>
- Speed, D., & Balding, D. J. (2015). Relatedness in the post-genomic era: Is it still useful? *Nature Reviews Genetics*, 16(1), 33–44. <https://doi.org/10.1038/nrg3821>
- Springate, D. A., & Kover, P. X. (2014). Plant responses to elevated temperatures: A field study on phenological sensitivity and fitness responses to simulated climate warming. *Global Change Biology*, 20(2), 456–465. <https://doi.org/10.1111/gcb.12430>
- Suding, K., Higgs, E., Palmer, M., Callicott, J. B., Anderson, C. B., Baker, M., Gutrich, J. J., Hondula, K. L., LaFevor, M. C., Larson, B. M. H., Randall, A., Ruhl, J. B., & Schwartz, K. Z. S. (2015). Committing to ecological restoration. *Science*, 348(6235), 638–640. <https://doi.org/10.1126/science.aaa4216>
- Sun, Y., Bossdorf, O., Grados, R. D., Liao, Z., & Müller-Schärer, H. (2020). Rapid genomic and phenotypic change in response to climate warming in a widespread plant invader. *Global Change Biology*, 26(11), 6511–6522. <https://doi.org/10.1111/gcb.15291>
- Supple, M. A., Bragg, J. G., Broadhurst, L. M., Nicotra, A. B., Byrne, M., Andrew, R. L., Widdup, A., Aitken, N. C., & Borevitz, J. O. (2018). Landscape genomic prediction for restoration of a *Eucalyptus* foundation species under climate change. *ELife*, 7, e31835. <https://doi.org/10.7554/eLife.31835>
- Thornton, P. E., Thornton, M. M., Mayer, B. W., Wei, Y., Devarakonda, R., Vose, R. S., & Cook, R. B. (2016). Daymet: Daily Surface Weather Data on a 1-km Grid for North America,

- Tibshirani, R. (1996). Regression Shrinkage and Selection via the Lasso. *Journal of the Royal Statistical Society. Series B (Methodological)*, 58(1), 267–288.
- Tienderen, P. H. van, Hammad, I., & Zwaal, F. C. (1996). Pleiotropic effects of flowering time genes in the annual crucifer *Arabidopsis thaliana* (Brassicaceae). *American Journal of Botany*, 83(2), 169–174. <https://doi.org/10.1002/j.1537-2197.1996.tb12693.x>
- Tilman, D., Clark, M., Williams, D. R., Kimmel, K., Polasky, S., & Packer, C. (2017). Future threats to biodiversity and pathways to their prevention. *Nature*, 546(7656), 73–81. <https://doi.org/10.1038/nature22900>
- van Vuuren, D. P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G. C., Kram, T., Krey, V., Lamarque, J.-F., Masui, T., Meinshausen, M., Nakicenovic, N., Smith, S. J., & Rose, S. K. (2011). The representative concentration pathways: An overview. *Climatic Change*, 109(1), 5. <https://doi.org/10.1007/s10584-011-0148-z>
- Weinig, C., Stinchcombe, J. R., & Schmitt, J. (2003). Evolutionary Genetics of Resistance and Tolerance to Natural Herbivory in *Arabidopsis thaliana*. *Evolution*, 57(6), 1270–1280. JSTOR.
- Wheeler, T. R., Craufurd, P. Q., Ellis, R. H., Porter, J. R., & Vara Prasad, P. V. (2000). Temperature variability and the yield of annual crops. *Agriculture, Ecosystems & Environment*, 82(1), 159–167. [https://doi.org/10.1016/S0167-8809\(00\)00224-3](https://doi.org/10.1016/S0167-8809(00)00224-3)
- Wilczek, A. M., Burghardt, L. T., Cobb, A. R., Cooper, M. D., Welch, S. M., & Schmitt, J. (2010). Genetic and physiological bases for phenological responses to current and predicted climates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1555), 3129–3147. <https://doi.org/10.1098/rstb.2010.0128>
- Wilczek, A. M., Cooper, M. D., Korves, T. M., & Schmitt, J. (2014). Lagging adaptation to warming climate in *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences*, 111(22), 7906–7913. <https://doi.org/10.1073/pnas.1406314111>
- Wilczek, A. M., Roe, J. L., Knapp, M. C., Cooper, M. D., Lopez-Gallego, C., Martin, L. J., Muir,

- C. D., Sim, S., Walker, A., Anderson, J., Egan, J. F., Moyers, B. T., Petipas, R., Giakountis, A., Charbit, E., Coupland, G., Welch, S. M., & Schmitt, J. (2009). Effects of Genetic Perturbation on Seasonal Life History Plasticity. *Science*, 323(5916), 930–934. <https://doi.org/10.1126/science.1165826>
- Wilson, A. J., Réale, D., Clements, M. N., Morrissey, M. M., Postma, E., Walling, C. A., Kruuk, L. E. B., & Nussey, D. H. (2010). An ecologist's guide to the animal model. *Journal of Animal Ecology*, 79(1), 13–26. <https://doi.org/10.1111/j.1365-2656.2009.01639.x>
- Windhausen, V. S., Atlin, G. N., Hickey, J. M., Crossa, J., Jannink, J.-L., Sorrells, M. E., Raman, B., Cairns, J. E., Tarekegne, A., Semagn, K., Beyene, Y., Grudloyma, P., Technow, F., Riedelsheimer, C., & Melchinger, A. E. (2012). Effectiveness of Genomic Prediction of Maize Hybrid Performance in Different Breeding Populations and Environments. *G3: Genes, Genomes, Genetics*, 2(11), 1427–1436. <https://doi.org/10.1534/g3.112.003699>
- Wortley, L., Hero, J.-M., & Howes, M. (2013). Evaluating Ecological Restoration Success: A Review of the Literature. *Restoration Ecology*, 21(5), 537–543. <https://doi.org/10.1111/rec.12028>
- Wu, X., Liu, H., Li, X., Tian, Y., & Mahecha, M. D. (2017). Responses of Winter Wheat Yields to Warming-Mediated Vernalization Variations Across Temperate Europe. *Frontiers in Ecology and Evolution*, 5. <https://doi.org/10.3389/fevo.2017.00126>
- Yu, H., Luedeling, E., & Xu, J. (2010). Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. *Proceedings of the National Academy of Sciences*, 107(51), 22151–22156. <https://doi.org/10.1073/pnas.1012490107>
- Zhang, J., Song, Q., Cregan, P. B., & Jiang, G.-L. (2016). Genome-wide association study, genomic prediction and marker-assisted selection for seed weight in soybean (*Glycine max*). *TAG. Theoretical and Applied Genetics. Theoretische Und Angewandte Genetik*, 129(1), 117–130. <https://doi.org/10.1007/s00122-015-2614-x>
- Zhang, X., Tarpley, D., & Sullivan, J. T. (2007). Diverse responses of vegetation phenology to a warming climate. *Geophysical Research Letters*, 34(19).

<https://doi.org/10.1029/2007GL031447>

Zhao, C., Liu, B., Piao, S., Wang, X., Lobell, D. B., Huang, Y., Huang, M., Yao, Y., Bassu, S., Ciais, P., Durand, J.-L., Elliott, J., Ewert, F., Janssens, I. A., Li, T., Lin, E., Liu, Q., Martre, P., Müller, C., ... Asseng, S. (2017). Temperature increase reduces global yields of major crops in four independent estimates. *Proceedings of the National Academy of Sciences*, 114(35), 9326–9331. <https://doi.org/10.1073/pnas.1701762114>

480