# Heritable and climatic sources of variation in juvenile tree growth in an Austrian common garden experiment of Central European Norway spruce populations

Laura Morales[1,2] and Kelly Swarts[1,3]*

[1]Gregor Mendel Institute, Austrian Academy of Sciences, Vienna BioCenter, Vienna, Austria

[2]Institute of Biotechnology in Plant Production, Department of Agrobiotechnology, University of Natural Resources and Life Sciences Vienna, Tulln, Austria

[3]Max Perutz Labs, University of Vienna, Vienna BioCenter, Vienna, Austria

*Corresponding: kelly.swarts@gmi.oeaw.ac.at

**Abstract**

We leveraged publicly available data on juvenile tree height of 299 Central European Norway spruce populations grown in a common garden experiment across 24 diverse trial locations in Austria and weather data from the trial locations and population provenances to parse the heritable and climatic components of tree height variation. Principal component analysis of geospatial and weather variables demonstrated high interannual variation among trial environments, largely driven by differences in precipitation, and separation of population provenances based on altitude, temperature, and snowfall. Tree height was highly heritable and genetic variation for tree height was strongly associated with climatic relationships among population provenances. Modeling the covariance between populations and trial environments based on climatic data increased the heritable signal for tree height.

## Introduction

Under rapid anthropogenic climate change, ecosystem dominant conifer species, such as Norway spruce (*Picea abies*), are facing environmental conditions to which they have not been adapted (Lindner et al. 2010; Seidl et al. 2017). Although Norway spruce has broad genetic diversity and geographic adaptation, long generation times and the confounded effects of population structure and local adaptation make breeding populations for new environments challenging (Leslie et al. 2012; Yeaman et al. 2016; Wang et al. 2020). Common garden experiments can be used to evaluate a select number of diverse individuals or populations in different environments (Oleksyn et al. 1998; Kapeller et al. 2012; Aitken and Bemmels 2016). Assisted migration can then be conducted, where well-adapted individuals are introduced into locations with compatible (current or forecasted) climates (Williams and Dumroese 2013; Aitken and Bemmels 2016).

Precise estimation of genetic and environmental effects on tree growth phenotypes is critical for assisted migration and breeding program selections (Williams and Dumroese 2013; Aitken and Bemmels 2016). In addition to proper experimental design, germplasm choice, and phenotyping methods, statistical approaches can also increase the genetic signal and prediction accuracy of

phenotypes (Heslot et al. 2015; Crossa et al. 2017; Isidro y Sánchez and Akdemir 2021). For example, leveraging genetic marker, geospatial, and/or climatic data to model relationships between individuals, trial locations, and genotype × environment interactions is a common approach in agricultural and forest genetics and breeding (Heslot et al. 2014; Crossa et al. 2016; Rodríguez-Álvarez et al. 2018; Avanzi et al. 2019; Bustos-Korts et al. 2019).

In this study, we combined publicly available datasets on (a) juvenile tree height from a common garden experiment of Norway spruce, in which 299 Central European populations were evaluated across five years in 24 locations in Austria and (b) monthly precipitation and temperature measurements from the common garden trial locations and population provenances (Efthymiadis et al. 2006; Hiebl et al. 2009; Chimani et al. 2011, 2013; Kapeller et al. 2012, 2017). Previous studies have used this dataset to understand varying selection and intraspecific variation in climate response from an ecological perspective (Kapeller et al. 2012, 2017). Here, we employed agricultural statistical methods to parse the heritable (genetic) and environmental components of phenotypic variance in tree height.

## Materials and methods

### *Common garden experiment*

We used a publicly available dataset to investigate population and environmental effects on juvenile tree growth in Norway spruce (*Picea abies*) (Nather and Holzer 1979; Schulze 1985; Kapeller et al. 2012, 2016, 2017). The plant material was derived from 299 Norway spruce populations collected across Central Europe during commercial seed harvests in 1971. Seeds from each population were germinated and seedlings were then transplanted into a nursery in Austria in 1973. In 1978, a total of 65,534 five-year-old trees were transplanted into 24 trial locations across Austria in a balanced incomplete block design. On average, each population was grown at two locations, 27 populations were grown in each location, and 102 trees (replications) from each population were split into three randomized blocks within each location. The height (cm) of each tree was recorded at the ages of 7-10 and 15 years in 1980-1983 and 1988, respectively, resulting in a total of 327,670 observations. The previously published dataset also included the altitude, latitude, and longitude for all trial locations and for 278 population provenances.

### *Weather data*

We accessed monthly precipitation (total, liquid, solid) and temperature data from the publicly available Historical Instrumental Climatological Surface Time Series of the Greater Alpine Region (HISTALP) resource (Efthymiadis et al. 2006; Hiebl et al. 2009; Chimani et al. 2011, 2013). The HISTALP dataset includes monthly temperature and precipitation grids from 1780-2009 and 1801-2003, respectively, at 5 min x 5 min resolution ranging from 4-19°E and 43-46°N. We extracted data from the original Network Common Data Form (NetCDF) formatted HISTALP files using the “netcdf4” package in R (R Core Team 2020; Pierce 2021).

### *Climatic analysis*

All altitude, latitude, longitude, and HISTALP weather variables used in the analyses described in this subsection were centered and scaled using the "scale" function in R (R Core Team 2020). We conducted principal component analysis (PCA) using the "FactoMineR" package in R (Lê et al. 2008; R Core Team 2020). To investigate spatiotemporal variation across the common garden experiment, we extracted monthly temperature and precipitation data from the grids closest to the trial locations in 1980-1983 and 1988 from the HISTALP dataset. We then conducted PCA using the altitude, latitude, longitude and monthly weather data from each trial location in each year, henceforth referred to as trial environments ($PCA_{Env}$). To explore climatic differences among population provenances, we extracted monthly temperature and precipitation data from the grids closest to the population provenances from 1801 (earliest year with both temperature and precipitation data in HISTALP) to 1970 (year before seed harvests). Weather data from this time period should reflect the climates experienced by the parental populations of the trees evaluated in the common garden experiment. We then conducted a PCA using the altitude, latitude, longitude, and monthly weather data from each population provenance ($PCA_{Prov}$).

### *Phenotypic analysis*

We used the "breedR" package in R (Muñoz and Sanchez 2020; R Core Team 2020) to fit the following basic phenotypic mixed model:

$$Height_{ijk} = \mu + Age + Pop_i + Env_j + Block[Env]_{jk} + PopEnv_{ij} + \varepsilon_{ijk} \tag{1}$$

where $Height_{ijk}$ is the tree height response, $\mu$ is the overall mean, $Age$ is the continuous fixed effect of tree age, $Pop_i$ is the random effect of population $i$, $Env_j$ is the random effect of trial environment (location-year) $j$, $Block[Env]_{jk}$ is the random effect of block $k$ nested within trial environment $j$, $PopEnv_{ij}$ is the random effect of the interaction between population $i$ and trial environment $j$, and $\varepsilon_{ijk}$ is the random error. The random effects were assumed to be independent and identically normally distributed, where $Pop_i \sim N(0, \boldsymbol{I}\sigma_p^2)$, $Env_j \sim N(0, \boldsymbol{I}\sigma_e^2)$, $Block[Env]_{jk} \sim N(0, \boldsymbol{I}\sigma_{b[e]}^2)$ , $PopEnv_{ij} \sim N(0, \boldsymbol{I}\sigma_{pe}^2)$, and $\varepsilon_{ijk} \sim N(0, \boldsymbol{I}\sigma_\varepsilon^2)$. We estimated $H^2$ as $H^2 = \frac{\sigma_P^2}{\sigma_p^2 + (\sigma_{pe}^2/n_e) + (\sigma_\varepsilon^2/n_e n_r)}$, where $n_e$ and $n_r$ are the number of trial environments ($n_e$ = 10) and replications ($n_r$ = 102) per population, respectively, and $\sigma_p^2$, $\sigma_{pe}^2$, and $\sigma_\varepsilon^2$ are the variance components for population, population × environment, and error, respectively (Holland et al. 2003; Piepho and Moehring 2007).

### *Phenotypic analysis using climatic data*

We used the altitude, latitude, longitude, and HISTALP weather data described previously to model the relationships among population provenances and environments (trial location-years). We first calculated Euclidian distance matrices using said geospatial and weather variables for all pairs of population provenances ($\boldsymbol{D}_{Prov}$) and trial environments ($\boldsymbol{D}_{Env}$) with the "dist" function

in R (R Core Team 2020). We then transformed the distance matrices into similarity matrices as $\boldsymbol{S}_{Prov} = \frac{\max(\boldsymbol{D}_{Prov}) - \boldsymbol{D}_{Prov}}{\max(\boldsymbol{D}_{Prov})}$ and $\boldsymbol{S}_{Env} = \frac{\max(\boldsymbol{D}_{Env}) - \boldsymbol{D}_{Env}}{\max(\boldsymbol{D}_{Env})}$ for further use in phenotypic modeling.

We tested the variance in tree height estimates for population and environment explained by climatic covariance (similarity) among population provenances (seed source locations) and trial environments, respectively. We extracted the population and environment best linear unbiased predictors (BLUPs) from model (1). We then fit the following mixed models:

$$popBLUP_i = \mu + Prov_i + \varepsilon_i \tag{2}$$

$$envBLUP_i = \mu + Env_i + \varepsilon_i \tag{3}$$

where $\mu$ is the overall mean, $popBLUP_i$ is the population BLUPs from model (1) as the response for model (2), $envBLUP_i$ is the environment BLUPs from model (1) as the response for model (3), $Prov_i$ is the random effect of population provenance $i$, $Env_i$ is the random effect of trial environment $i$, and $\varepsilon_i$ is the random error. The random effects were distributed as $Prov_i \sim N(0, \boldsymbol{S}_{Prov}\sigma_p^2)$, $Env_i \sim N(0, \boldsymbol{S}_{Env}\sigma_e^2)$, and $\varepsilon_i \sim N(0, \boldsymbol{I}\sigma_\varepsilon^2)$.

We then tested the use of the similarity matrices in phenotypic modeling for tree height. Due to the large number of observations (N=327,670) in the common garden experiment, it was not computationally feasible to specify these complex variance-covariance matrices for the entire dataset in one model. As such, we used a two-stage approach common in plant breeding and genetics studies, with mixed linear models fit with the “breedR” package in R (Muñoz and Sanchez 2020; R Core Team 2020). In the first stage, we fit the following mixed model within each environment (location-year):

$$Height_{ij} = \mu + Pop_i + Block_j + \varepsilon_{ij} \tag{4}$$

where $Height_{ij}$ is the tree height response, $\mu$ is the overall mean, $Pop_i$ is the fixed effect of population $i$, $Block_j$ is the random effect of block $j$, and $\varepsilon_{ij}$ is the random error. The random effects were independent and identically normally distributed as $Block_j \sim N(0, \boldsymbol{I}\sigma_b^2)$ and $\varepsilon_{ij} \sim N(0, \boldsymbol{I}\sigma_\varepsilon^2)$. We then extracted the fitted values ($\hat{y}_{ij}$) for each population $i$ within each block $j$ from each within-environment model (4) as

$$\hat{y}_{ij} = popBLUE_i + blockBLUP_j \tag{5}$$

where $popBLUE_i$ is the best linear unbiased estimate of population $i$ and $blockBLUP_j$ is the best linear unbiased predictor of block $j$. We combined the fitted values across environments, resulting in a reduced and refined set of phenotypes for further analysis (N=7,314). Only fitted

values for populations with climatic information were included in the second stage of the analysis (278/299 populations). In the second stage, we fit a naive mixed model with the form:

$$\hat{y}_{ij} = \mu + Pop_i + Env_j + PopEnv_{ij} + \varepsilon_{ij} \tag{6}$$

where $\hat{y}_{ij}$ are the fitted values from each within-environment model (5), $\mu$ is the overall mean, $Pop_i$ is the random effect of population $i$, $Env_j$ is the random effect of trial environment $j$, $PopEnv_{ij}$ is the random effect of the interaction between population $i$ and trial environment $j$, and $\varepsilon_{ij}$ is the random error. The random effects were assumed to be independent and identically normally distributed, where $Pop_i \sim N(0, \boldsymbol{I}\sigma_p^2)$, $Env_j \sim N(0, \boldsymbol{I}\sigma_e^2)$, $PopEnv_{ij} \sim N(0, \boldsymbol{I}\sigma_{pe}^2)$, and $\varepsilon_{ij} \sim N(0, \boldsymbol{I}\sigma_\varepsilon^2)$.

In the second stage, we also fit a mixed model with form similar to model (6):

$$\hat{y}_{ij} = \mu + Prov_i + Env_j + ProvEnv_{ij} + \varepsilon_{ij} \tag{7}$$

where $\hat{y}_{ij}$ are the fitted values from each within-environment model (5), $\mu$ is the overall mean, $Prov_i$ is the random effect of population provenance $i$, $Env_j$ is the random effect of trial environment $j$, $ProvEnv_{ij}$ is the random effect of the interaction between population provenance $i$ and trial environment $j$, and $\varepsilon_{ij}$ is the random error. The random effects were distributed as $Prov_i \sim N(0, \boldsymbol{S}_{Prov}\sigma_p^2)$, $Env_j \sim N(0, \boldsymbol{S}_{Env}\sigma_e^2)$, $ProvEnv_{ij} \sim N(0, \boldsymbol{I}\sigma_{pe}^2)$, and $\varepsilon_{ij} \sim N(0, \boldsymbol{I}\sigma_\varepsilon^2)$. In model (7), we used the term “population provenance” rather than “population” for two reasons: (i) to distinguish model (7) from model (6) and (ii) the population variance was modeled as the similarity matrix estimated from climatic data from the provenances (seed source locations) of the populations.

For the second stage models, we estimated $H^2$ as $H^2 = \frac{\sigma_P^2}{\sigma_p^2 + (\sigma_{pe}^2/n_e) + (\sigma_\varepsilon^2/n_e n_r)}$, where $n_e$ and $n_r$ are the number of trial environments ($n_e$ = 10) and replications ($n_r$ = 50) per population provenance, respectively, and $\sigma_p^2$, $\sigma_{pe}^2$, and $\sigma_\varepsilon^2$ are the variance components for population provenance, population provenance × environment, and error, respectively (Holland et al. 2003; Piepho and Moehring 2007).

## Results

### *Climatic and geospatial variation among trial environments and population provenances*

In a PCA using geospatial and weather data from trial environments (location-years), the first and second principal components (PCs) explained 28% and 21% of the variance, respectively (Figure 1). The first PC demonstrated a separation between environments based on altitude and monthly temperature, while environments were separated by year and monthly precipitation on the second PC (Figure 1).

We also conducted PCA for populations provenances using geospatial and weather data. The first PC explained 44% of the variance and separated provenances largely based on altitude (Figure 2). The second PC showed some separation between population provenances with respect to latitude, explaining 23% of the variance (Figure 2). In addition, the eigenvectors of the PCA predictor variables demonstrated that variation in PC 1 was driven by altitude, temperature, and snowfall (solid precipitation), while variation in PC 2 was driven by rainfall (liquid precipitation).

### *High heritability for juvenile tree growth*

In a basic phenotypic model for tree height, population, block[environment], and population × environment each explained a small proportion (<5%) of the total variance in juvenile tree height, while 58% of the total variance was explained by environment (Table 1). Although population variance was low, the highly replicated experimental design allowed for a high estimation of broad-sense heritability for tree height ($H^2 = 0.73$). Year had an effect estimate of 22.30 ± 1.44 cm, meaning that each tree grew an average of 22 cm per year.

### *Climate explains environmental variance in tree height*

Because the common garden experiment consisted of even-aged stands planted at the same time across trial locations, tree age (physiological growth stage) and trial environment (location-year) may have been confounded. As such, we tested the variance in environment BLUPs for tree height explained by climatic similarity between trial environments. The environmental similarity matrix, estimated from climatic and geospatial data across trial location-year environments, explained 95% of the variance in environmental BLUP estimates for tree height. The predicted values from said model were highly correlated (r = 0.99) with the actual environment BLUPs (Figure 2). These results suggest that the variation in tree height among trial location-year environment estimates is largely driven by climatic and geospatial differences rather than confounding effects of tree growth stage.

### *Variation in tree height among populations explained by population provenance climate*

The population provenance similarity matrix, estimated from climatic and geospatial data across population provenances, explained 44% of the variance in populations BLUPs for tree height, with a high correlation (r = 0.63) between the predicted values and observed population BLUPs (Figure 2). These results indicate a strong signal of local adaption.

### *Climatic modeling increases heritable signal for juvenile tree height*

We conducted a two-stage phenotypic analysis, in which we (1) estimated tree height values, correcting for population and block effects within environments and then (2) used the refined tree height estimates (fitted values) as the response for phenotypic modeling. The phenotypic modeling in the second stage included a naive model with independent and identically distributed random effects. In the naïve model, population and population × environment explained 1% and 2% of the total variance in tree height, respectively, while environment accounted for 96% of the variance in tree height (Table 1). We also fit a model in the second

stage in which the variance-covariance of the population and environment random effects were modeled as the climatic similarity matrices between population provenances and trial environments, respectively. In the second-stage model with specified provenance and environment variance-covariance, population provenance explained a greater proportion of the total variance in tree height (5%) than in the naïve model (Table 1), while the variance explained by provenance × environment (2%) and environment (92%) were similar to the naïve model (Table 1). Broad-sense heritability for tree height was higher in the model with specified variance-covariance ($H^2$ = 96%) than in the naïve model ($H^2$ = 0.82).

## Discussion

We used agricultural statistical methods to dissect the heritable and environmental components of juvenile tree growth in Central European Norway Spruce. The highly replicated design of the common garden experiment allowed for precise estimation of genetic (population and population × environment) and environmental (trial location-year, block) effects. Although population explained a small proportion of the total variance in tree height (1-5%), similar to previous findings in this dataset (Kapeller et al. 2017), broad-sense heritability was high (0.73-0.96). Modeling the variance-covariance of population and environment using climate data increased genetic variance and heritability for tree height. Plant and animal breeders frequently use climate and/or genetic marker data to model relationships among individuals and/or environments in order to improve the prediction accuracy of phenotypic models (Heslot et al. 2014; Crossa et al. 2016; Bustos-Korts et al. 2019). The modeling used in this study results in refined tree growth estimates for population and population × environment, which could be used to identify potential sources of material adapted to new environments.

We found that climatic relationships among population provenances were closely linked with interpopulation tree height variation, demonstrating that these populations have strong local adaptation (Aitken and Bemmels 2016). Our findings support previous results from ecological modeling, where within-population variation was driven by population provenance temperature (Kapeller et al. 2017). Differences among trial location-year environments were largely driven by interannual climatic variation rather than geospatial relationships. Because only a limited number of genetic sources can be evaluated in common garden experiments, these results suggest that increasing the number of years of observation per trial location may effectively increase the number of climatically distinct environments observed in an experiment.

## Tables and figures

Figure 1. Plots of the fist and second principal components (PCs) from principal component analysis (PCA) of trial environments based on geospatial and climatic data. Trial environments were labeled based on (A) a combination of altitude, longitude, and latitude and (B) year. Eigenvectors for the geospatial and weather predictors of the PCA are shown in (B).

Figure 2. (A) Plot of the fist and second principal components (PCs) from principal component analysis (PCA) of population provenances based on geospatial and climatic data. (B) Map of

population provenance. Points were labeled based on a combination of altitude, longitude, and latitude.

Table 1. Number of levels and estimated variances for population/provenance, environmental, and residual random effects from tree height phenotypic models.

| **Model** | **Term** | **Estimated variance ± standard error** | **Proportion of total variance** | **Levels** |
|---|---|---|---|---|
| Basic | Population | 55.26 ± 6.15 | 0.022 | 299 |
| | Environment | 1479.4 ± 202.83 | 0.579 | 641 |
| | Block[Environment] | 65.28 ± 6.52 | 0.026 | 360 |
| | Population × Environment | 126.37 ± 3.81 | 0.049 | 3205 |
| | Error | 829.08 ± 2.15 | 0.324 | |
| Two-stage, naive | Population | 56.65 ± 6.51 | 0.011 | 278 |
| | Environment | 4737.6 ± 634.22 | 0.955 | 113 |
| | Population × Environment | 109.1 ± 4.01 | 0.022 | 2871 |
| | Error | 59.81 ± 1.29 | 0.012 | |
| Two-stage, specified var-cov | Provenance | 56.65 ± 6.51 | 0.050 | 278 |
| | Environment | 4737.6 ± 634.22 | 0.920 | 113 |
| | Provenance × Environment | 109.1 ± 4.01 | 0.020 | 2871 |
| | Error | 59.81 ± 1.29 | 0.010 | |

Basic: model 1; two-stage, naive: model 4; two-stage, specified var-cov: model 5

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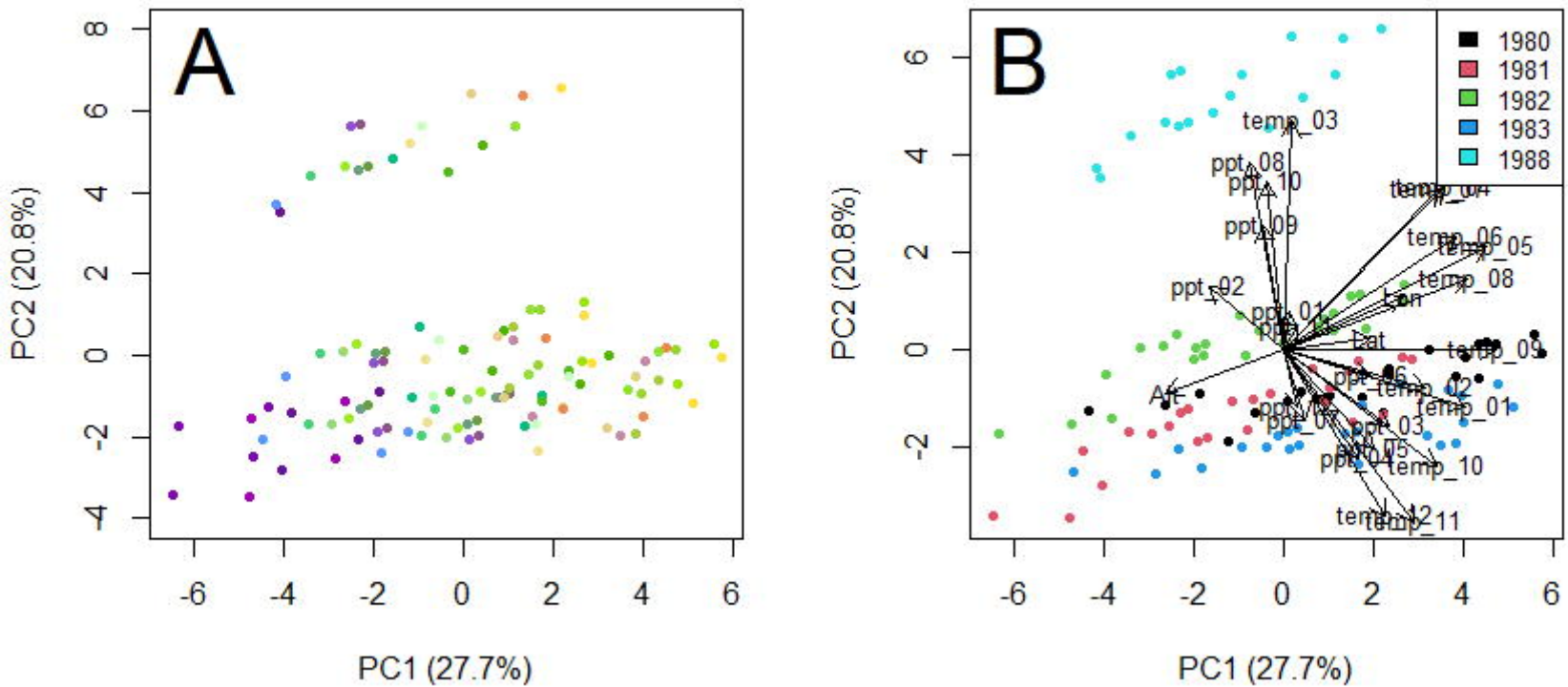
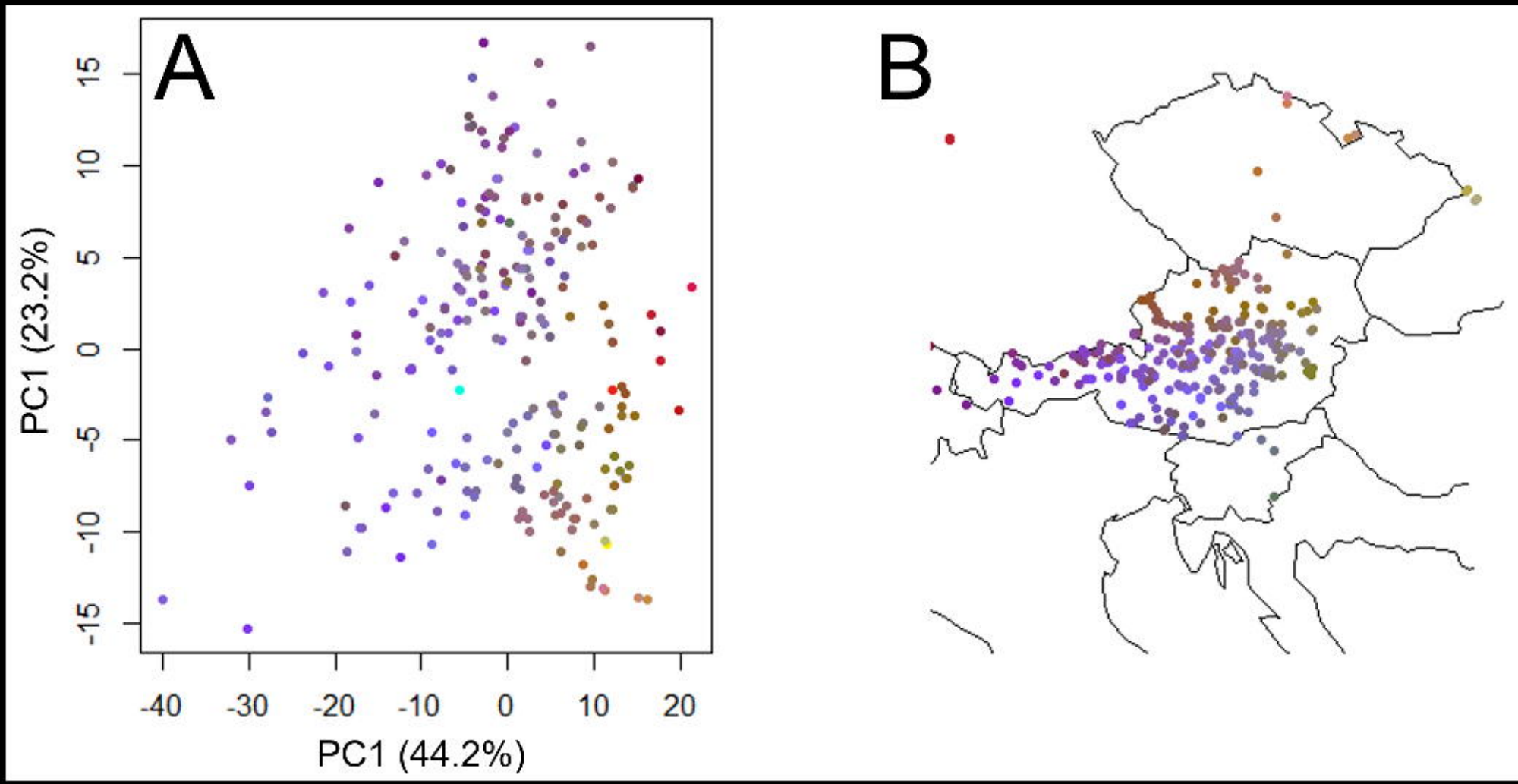

A
B
PC1 (27.7%)
PC2 (20.8%)
1980
1981
1982
1983
1988
temp_03
ppt_08
ppt_10
ppt_09
ppt_02
ppt_01
temp_06
temp_05
temp_08
Lon
Lat
temp_09
temp_02
temp_01
ppt_03
temp_10
temp_11
Alt


A
B
PC1 (23.2%)
PC1 (44.2%)
15
10
5
0
-5
-10
-15
-40
-30
-20
-10
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10
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