Evaluating genomic offset predictions in a forest tree with high population genetic structure

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Abstract

Genomic offset models are increasingly popular tools for identifying populations at risk of maladaptation under climate change. These models estimate the extent of genetic change required for populations to remain adapted under future climate change scenarios, but face strong limitations and still lack broad empirical testing. Using 9,817 single nucleotide polymorphisms (SNPs) genotyped in 454 trees from 34 populations of maritime pine, a species with a marked population genetic structure, we found substantial variability across genomic offset predictions from different methods, SNP sets, and general circulation models. Using five common gardens, we mostly found positive associations between genomic offset predictions and mortality, as expected. However, contrary to our expectations, we observed very few negative monotonic associations between genomic offset predictions and height. Higher mortality rates were also observed in national forest inventory plots with high genomic offset, but only for some methods and SNP sets. The differing genomic offset patterns produced by the best-validated methods across the maritime pine range hindered drawing definitive conclusions for the species. Our study demonstrates the imperative of employing different methods and validating genomic offset predictions with independent data sources before using them as reliable metrics to inform conservation or management.

1 Introduction

Mounting evidence shows that anthropogenic climate change is already affecting biodiversity (Parmesan and Yohe 2003), exposing populations and species to unprecedented risks

of decline and extinction (Urban 2015, Wiens 2016). By shifting fitness optima, climate change increases the mismatch between the current phenotypes of well-adapted populations and their environment, thereby decreasing the average fitness of the populations (i.e., scenario of the moving target in Brady et al. 2019a). The consequent maladaptation can be counterbalanced by sufficient and appropriate adaptive variation, which can enable rapid evolution towards the new phenotypic optimum (Brady et al. 2019b). However, if the extent and rate of climate change are too severe, the demographic costs of maladaptation might be too high relative to the capacity and speed of adaptation, and populations will be pushed toward extinction (Bürger and Lynch 1995, Gomulkiewicz and Holt 1995, Chevin et al. 2010, Uecker et al. 2014).

To identify populations at risk of short-term maladaptation under climate change, Fitzpatrick and Keller (2015) developed the concept of genomic offset (or genetic offset). They modeled the non-linear turnover in allele frequencies along climatic gradients with two approaches from community-level modeling, namely Gradient Forest (GF; Ellis et al. 2012) and Generalised Dissimilarity Modeling (GDM; Ferrier et al. 2007). They then calculated the genomic offset as the distance between the current genomic composition of the populations and the genomic composition required to maintain the estimated gene-climate relationships (Fitzpatrick and Keller 2015). Since then, genomic offset has been estimated with a variety of other methods including Redundancy Analysis (RDA; Capblancq and Forester 2021), the Risk Of Non Adaptedness (RONA; Rellstab et al. 2016) and Latent Factor Mixed Model (LFMM; Gain and François 2021). As they are straightforward to implement (genomic and climatic data from several populations are sufficient) and seemingly easy to interpret, these methods have already been applied to a wide range of species, and genomic offset

predictions are now beginning to be recommended to guide management and conservation strategies (e.g., Rhoné et al. 2020, Lachmuth et al. 2023, Yuan et al. 2023).

In this context, it is crucial to emphasize that genomic offset is not informative about the capacity of populations to adapt, i.e., to evolve towards the new fitness optima of future climates, and therefore captures only part of the vulnerability of populations to climate change (IPCC 2007, Foden et al. 2019). Moreover, the genomic offset concept relies on strong assumptions that undermine the robustness of its predictions (Rellstab et al. 2021, Ahrens et al. 2025). One key assumption is that populations are currently optimally adapted to their local environment, which is often violated. For instance, populations of temperate and boreal tree species at the northern edges of their distribution would benefit from a temperature increase, at least in the short term (Rehfeldt et al. 2002, 2003, Savolainen et al. 2007, Pedlar and McKenney 2017, Rehfeldt et al. 2018, Fréjaville et al. 2020). Another key assumption is that populations from different geographic locations but occupying similar environments have the same adaptive alleles; but the same phenotypes can be produced by multiple different combinations of genetic variants (i.e., 'genotypic redundancy'; Láruson et al. 2020) and how populations evolve towards the fitness optimum depends on the shape of the adaptive landscape (Lotterhos 2023). Genomic offset predictions are thus impacted by trait genomic architecture and the environmental landscape, as demonstrated in a simulation study based on the GF method (Láruson et al. 2022). The study also showed that the predicted rate of allele frequency change did not reflect the steepness of adaptive clines, when simulated as linear, although it did capture the extent to which the environmental gradient explained the turnover in allele frequencies (Láruson et al. 2022). Lastly, it is important to note that this approach is inherently correlative, and therefore subject to the

limitations typical of correlative methods, including limited control over confounding factors, lack of mechanistic understanding, poor predictive power under novel conditions, and the inability to establish causal relationships.

Neutral evolutionary and demographic processes also impact genomic offset predictions and how to account for them remains unclear. In particular, greater genetic drift in small populations results in greater allele turnover (Wright 1931), and thus higher genomic offset predictions without any selection pressure being involved (Láruson et al. 2020). Then, to avoid the confounding effects of population genetic structure, it was initially recommended to predict genomic offset based on a set of genetic markers previously identified as potentially involved in climate adaptation (Fitzpatrick and Keller 2015, Fitzpatrick et al. 2018), e.g., using gene-environment association (GEA) analyses correcting for population genetic structure. However, when patterns of demographic and adaptive history are confounded (e.g., species that migrated along climatic gradients after the last glaciation), correcting for population genetic structure is likely to hamper the detection of climate adaptation signals, and adopting a less strict approach to the selection of genetic markers might be more appropriate (Capblancq et al. 2023). Moreover, some studies have suggested that genomic offset can be predicted equally well by all or random sets of loci, thus questioning the relevance of prior selection of a set of candidate loci (Láruson et al. 2022, Lind et al. 2024, Lind and Lotterhos 2025). Finally, the uncertainty in genomic offset predictions also stems from the inherent uncertainty in future climate forecasts, which comes from unknowns in future greenhouse gas emission scenarios (which depends on socioeconomic factors, technological advancements, and policy decisions), internal climate variability (which hinders the estimation of long-term climate trends), uncertainty in the magnitude and timing of external forcings (e.g., volcanic

eruptions, changes in solar radiation), as well as uncertainty in the parameterization, process representation, simplifications and approximations of the general circulation models used to simulate the Earth's climate system (Collins et al. 2013).

Despite these limitations, genomic offset has gained support from empirical and simulation studies, which have consistently found the expected negative relationship between fitness proxies and genomic offset in common gardens (e.g., Capblancq and Forester 2021, Fitzpatrick et al. 2021, Láruson et al. 2022, Lind et al. 2024). While this relationship is typically weak in empirical studies, genomic offset predictions often outperformed climate or geographic distances (e.g., Capblancq and Forester 2021, Fitzpatrick et al. 2021, Lind et al. 2024). However, genomic offset models have still to be validated across a wider range of biological scenarios, species and methodological approaches. Simulation studies are crucial for defining the domain of applicability of the models and have already shown that genomic offset models perform poorly under certain scenarios, such as under climate novelty (Lind and Lotterhos 2025). Robust empirical evaluations are still rare, as they require carefully designed experiments with appropriate evaluation models, metrics and fitness proxies (Lotterhos 2024b). To date, most empirical evaluations have focused on predicting local-foreign fitness offsets in common gardens (i.e., assessing the relative fitness of different genotypes or populations within the same environment), which are more relevant for evaluating the success of restoration projects (Lotterhos 2024a). However, good predictive performance in such evaluations may not necessarily translate into accurate predictions of the maladaptation risk of natural populations to future climates (i.e., home-away fitness offsets; Lotterhos 2024a). Additionally, most empirical evaluations have used tree height as a fitness proxy, though this trait might not represent well fitness under certain conditions in forest trees

(Stephenson et al. 2011, Philipson et al. 2014). In parallel with experimental validation, developing methods to validate genomic offset using observational data in natural conditions (therefore estimating home-away fitness offsets) would be highly valuable. An interesting attempt in this direction is the study by Bay et al. (2018), which found that higher genomic offset predictions were associated with declining population sizes over the past half-century in a North American migratory bird. However, this association may also reflect increased genetic drift in declining populations, and therefore population sizes cannot be used directly as fitness proxies to evaluate genomic offset predictions (Fitzpatrick et al. 2018, Láruson et al. 2022, Lotterhos 2024b).

In this study, we evaluated the consistency and empirical validity of genomic offset predictions in maritime pine (*Pinus pinaster* Ait., Pinaceae), a tree species with fragmented populations in southwestern Europe and North Africa and a strong neutral population genetic structure (Alberto et al. 2013, Jaramillo-Correa et al. 2015), following the conceptual approach summarised in fig. 1. Our study relies on two main data sources (gray boxes in fig. 1):

(i) A network of five clonal common gardens planted in contrasted environments (the CLONAPIN network), in which 454 clones (replicated eight times in each common garden) from 34 populations were genotyped for 9,817 single nucleotide polymorphisms (SNPs) after filtering, and measured for height and mortality.

(ii) 11,917 plots from the French and Spanish national forest inventories (NFI) in which mortality rates were recorded.

Using these data, we addressed three key questions regarding genomic offset predictions (green boxes in fig. 1):

Q1. Consistency? Based on genomic data from the 454 clones of the common gardens and climatic data from their populations of origin, we evaluated the variability in genomic offset predictions under future climates using five methods (namely GF, RDA, partial RDA, GDM and LFMM), six SNP sets, and five climate general circulation models.

Q2. Empirical validity in common gardens? We tested whether populations with higher genomic offset in common gardens (i.e., local-foreign fitness offsets) exhibit higher mortality (i.e., a positive association with mortality) and lower growth (i.e., a negative association with height).

Q3. Empirical validity in natural populations? We tested whether inventory plots with higher genomic offset (i.e., home-away fitness offsets) show higher mortality rates (i.e., a positive association with mortality).

By answering these questions, we aimed to identify the genomic offset methods that provide the most robust and reliable predictions in our study system and subsequently use those predictions to gain insights into the risk of climate maladaptation in maritime pine. We also investigated how to account for population genetic structure. Finally, we discussed the role and limitations of genomic offset predictions to inform conservation and management of natural populations, and how they can be used effectively.

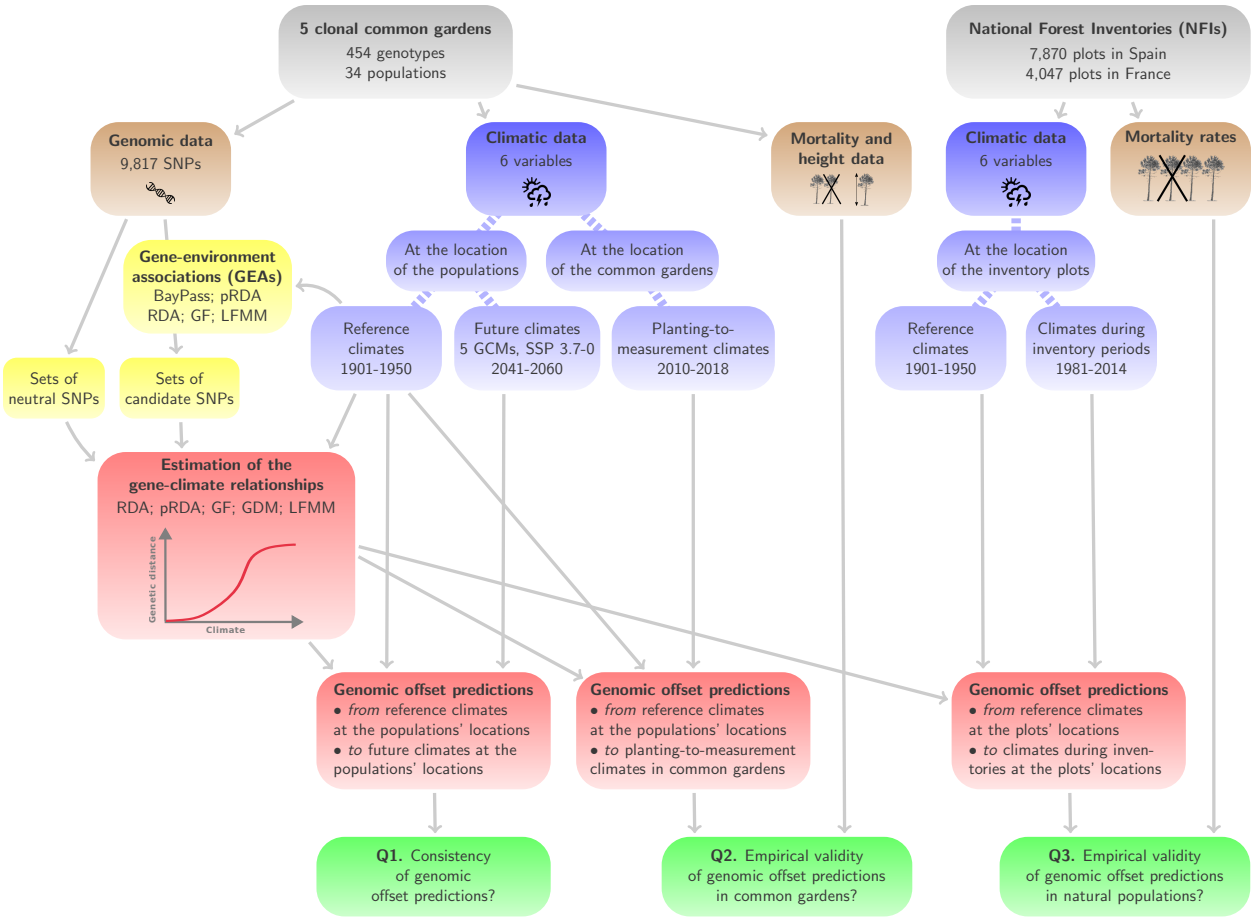

Figure 1: Conceptual representation of the study design. The two gray boxes at the top represent the two primary data sources of the study: the CLONAPIN clonal common garden network (section 2.2) and the national forest inventories (section 2.3). The brown boxes represent genomic, mortality and height data collected from these data sources. The blue boxes indicate climatic data obtained from the Climate Downscaling Tool (https://www.ibbr.cnr.it/climate-dt/; section 2.4). The yellow boxes show the sets of single nucleotide polymorphisms (SNPs) analyzed: three sets of control SNPs and three sets of candidate SNPs identified with five gene-environment association (GEA) methods. The red boxes represent the two steps applied to each of the five genomic offset methods: first, estimating the gene-climate relationships for each SNP set, and second, predicting the genomic offset using three different approaches: (1) for the 34 studied populations, using reference climates and future climates at the populations' locations (section 2.7); (2) for the 34 studied populations, using reference climates at the populations' locations and climates at the common garden locations between planting and measurement dates (section 2.8.1); and (3) for the 11,917 inventory plots, using reference climates and climates during the inventory periods at the plot locations (section 2.8.2). These genomic offset predictions addressed the three key research questions of the study (green boxes). Acronyms: GCMs for general circulation models, SSP for shared socio-economic pathway, RDA for Redundancy Analysis, pRDA for partial RDA, GF for Gradient Forest, GDM for Generalised Dissimilarity Modeling and LFMM for Latent Factor Mixed Model.

2 Materials & Methods

2.1 Focal species

Maritime pine is a wind-pollinated, outcrossing and long-lived tree species with large economic and ecological importance in southwestern Europe and North Africa. The species is widely exploited for its wood, and has a key role stabilizing coastal and fossil dunes and, as a foundation species, supporting biodiversity (Viñas et al. 2016). Natural populations of maritime pine are scattered over a large range of climatic conditions: the dry climate along the northern coasts of the Mediterranean Basin (from southern Spain to western Italy), the mountainous climates of southeastern Spain and Morocco (Rif and Atlas mountains), the wetter climate of the Atlantic region (from northwestern Spain and Portugal to the southwestern part of France), and the continental climate of central Spain (fig. 2). Maritime pine populations are also found on a wide range of substrates (from sandy and acidic soils to more calcareous ones) and in fire-prone regions, showing intraspecific variability in fire-related traits such as early flowering and serotiny (Tapias et al. 2004, Budde et al. 2014). Maritime pine is therefore a particularly interesting species for studying local adaptation and several studies have already provided evidence of genetic differentiation for adaptive traits (e.g., González-Martínez et al. 2002, de Miguel et al. 2022).

Eight gene pools and two isolated populations were recently identified in maritime pine by Theraroz et al. (2024) supporting previous reports of strong population genetic structure in this species (e.g., Alberto et al. 2013, Jaramillo-Correa et al. 2015). The sampled populations originated from six of these main gene pools, each probably originating from an unique glacial

refugia (Bucci et al. 2007, Santos-del-Blanco et al. 2012).

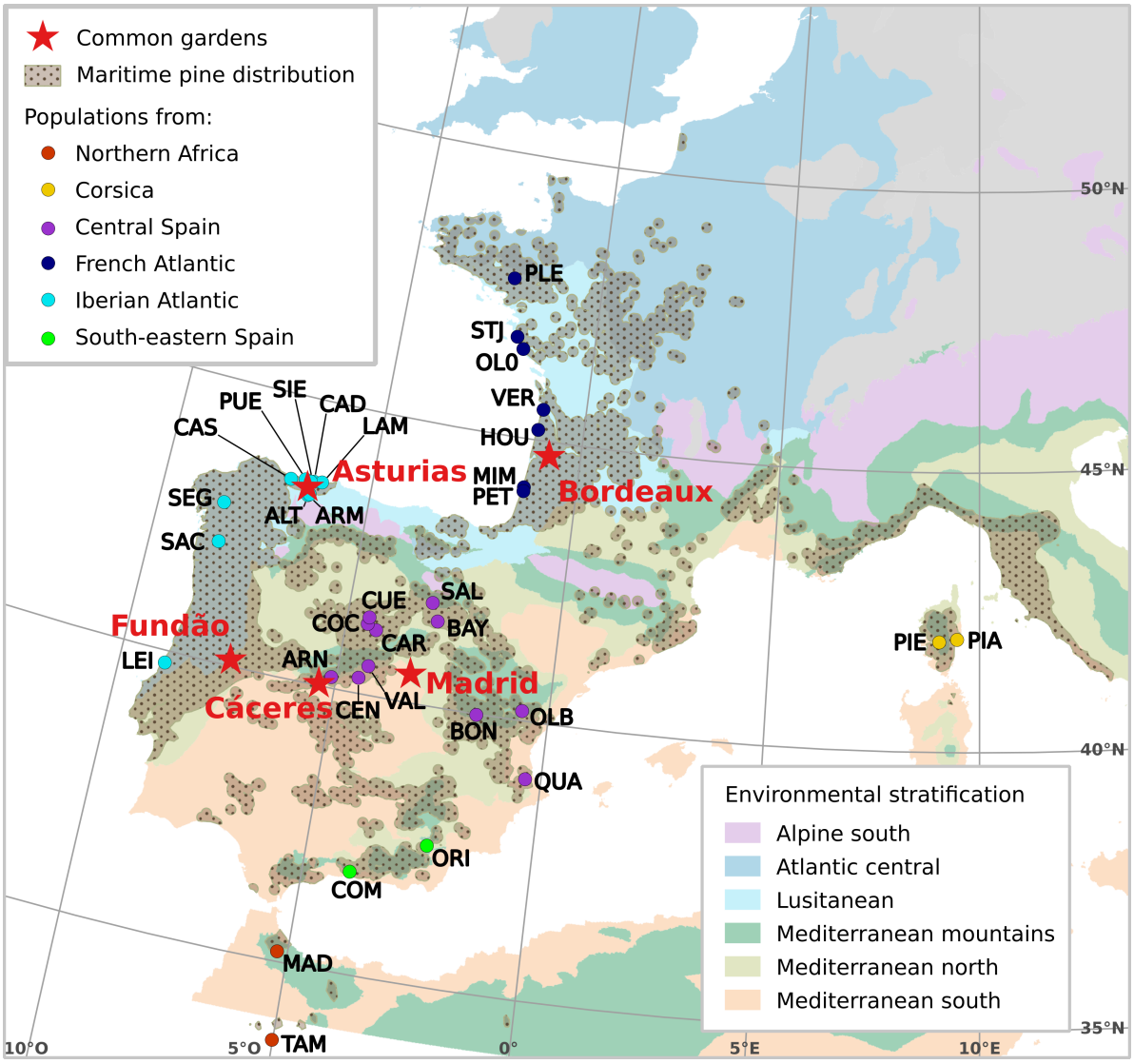

Figure 2: Location of the 34 genotyped maritime pine populations (filled dots) and the five common gardens (red stars) used in the validation steps and in which the same 34 populations were planted (CLONAPIN network). Populations are colored according to the main gene pool to which they belong, as estimated using the STRUCTURE software in Jaramillo-Correa et al. (2015). The environment stratification from Metzger (2018) is a statistically derived land classification that distinguishes environmental zones. We included it in the background of the map to highlight the variety of environments inhabited by maritime pine. The maritime pine distribution depicted in the figure combines the widely-used EUFORGEN map (http://www.euforgen.org/) and 10-km radius areas around the French and Spanish national forest inventory (NFI) plots with maritime pine occurrence. These plots were surveyed between 2000 and 2014 for the French inventory and between 1986 and 2008 for the Spanish inventory.

2.2 Clonal common garden network (CLONAPIN)

We used genomic, mortality and height data from 454 clones (i.e., genotypes) representing 34 populations (13 genotypes per population on average; table S1) and grown in a network of five clonal common gardens (CLONAPIN; fig. 2). These clones were obtained from open-pollinated seeds collected in natural populations and vegetatively propagated by cuttings (eight clonal replicates per genotype in each common garden; see details in de Miguel et al. 2022). Two trial sites, Asturias (Spain) and Bordeaux (France), benefit from the favorable climates of the Atlantic European region (i.e., mild winters, high annual rainfall and relatively wet summers; table S2) and have low proportions of dead trees ($\sim$ 2.8% and $\sim$ 3.6%, respectively; tables S3, S4). Two trial sites, Cáceres and Madrid (both in central Spain), experienced a strong drought during the summer following planting, worsened by the presence of clay soils and leading to the death of 92% and 72% of the trees, respectively (tables S3, S4). The last trial site, Fundão (Portugal), is located on the border between the Atlantic and Mediterranean climates, and thus also experiences relatively dry summers (table S2), leading to the mortality of $\sim$ 36.3% of the trees (tables S3, S4). Height and mortality were measured when the trees were 37 months old in Asturias, 85 months old in Bordeaux, 8 months old in Cáceres, 13 months old in Madrid and 27 months old in Fundão (table S5).

One ramet of each clone in the Asturias common garden were genotyped with the Illumina Infinium assay described in Plomion et al. (2016) and with the new ThermoFisher 4TREE multispecies Axiom assay (Guilbaud et al. 2020, Theraroz et al. 2024). We applied the following filtering steps in this order: individuals with more than 18% missing data across SNPs, SNPs with minor allele frequency below 1%, and SNPs with more than 20% missing

data across individuals. It resulted in 9,817 high-quality polymorphic SNPs, of which 2,855 were genotyped by both assays to ensure sample identity and estimate genotyping errors.

2.3 National forest inventory data

For genomic offset validation using natural populations (section 2.8.2), we used mortality data from the French and Spanish national forest inventory plots harmonised in Changenet et al. (2021) and covering the period 2000-2014 for the French inventory (4,047 plots) and 1986-2008 for the Spanish inventory (7,870 plots). Diameter at breast height (1.30 m, DBH) of maritime pines ranged from 10 to 263 cm, hence including both saplings and adult trees, and serves as a proxy for tree age. Basal area (C) of all tree species in a plot is a common proxy for competition among trees.

2.4 Climatic data

Climatic data at the location of the populations, common gardens and inventory plots were extracted from the Climate Downscaling Tool (Marchi et al. 2024). Six variables were selected based on their biological relevance for maritime pine, contribution to genetic variance (via RDA-based stepwise selection; table S6) and the magnitude of their exposure to climate change (fig. S1 and more details in section 2 of the Supplementary Information): mean annual temperature (*bio1*), isothermality (*bio3*, ratio of mean diurnal temperature range to annual temperature range), temperature seasonality (*bio4*), annual precipitation (*bio12*), precipitation seasonality (*bio15*) and summer heat moisture (*SHM*) index (table S7 and fig. S2).

We used the climate for the period 1901–1950 as reference climate for all genomic offset predictions (fig. 1, table 1). To predict the genomic offset under future climates (section 2.7, first column of table 1), we used the climatic forecasts for the period 2041-2060 under the shared socio-economic pathway (SSP) 3.7-0 and from five general circulation models, namely GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0 and UKESM1-0-LL. To predict the genomic offset in the common gardens (section 2.8.2; second column of table 1), we used the climate between the planting date and the measurement date for each common garden. To predict the genomic offset in the inventory plots (section 2.8.2; third column of table 1), we used the climate under which mortality rates were recorded, along with the climate of the five preceding years, to account for potential lag effects of climatic conditions on tree mortality. In the French inventory, a tree was considered dead if its death occurred within the five years prior to the inventory date, so we used the ten years preceding the inventory as the prediction period. For the Spanish inventory, the prediction period included the five years preceding the first inventory and the duration between the two inventories.

We also computed climate distances to compare with genomic offset predictions. Specifically, for each genomic offset prediction presented in table 1, we calculated the corresponding absolute climate distance. These distances were computed for each climatic variable independently and for all variables combined (Euclidean distances). For common gardens, we refer to these as climate transfer distances (CTDs), following common practice in the field.

	Genomic offset predictions under future climates	Genomic offset predictions in common gardens	Genomic offset predictions in natural populations
Prediction units	34 studied populations	34 studied populations	11,917 inventory plots
Reference climate	1901-1950 at the location of the populations	1901-1950 at the location of the populations	1901-1950 at the location of the plots
Prediction climate	Future climate at the location of the populations (five general circulation models; SSP 3.7-0; 2041-2060)	Climate between the planting and the measurement dates at the location of the common gardens (2010-2018)	Climate during the inventory period at the location of the French (1995-2014) and Spanish (1981-2008) plots
Gene-climate relationships	Estimated using the genomic composition and the 1901-1950 climate of the 34 studied populations		
Goal	Evaluate consistency (Q1)	Evaluate empirical validity in common gardens (Q2)	Evaluate empirical validity in natural populations (Q3)
Section in the manuscript	Section 2.7	Section 2.8.1	Section 2.8.2

Table 1: Genomic offset prediction approaches used in this study. See table 3 for a description of the methods used to predict the genomic offset.

2.5 Partitioning of the genetic variance

Predicting climate maladaptation is only meaningful if climate explains a portion of the genomic variation. To verify this fundamental assumption, we followed the methodology from Capblancq and Forester (2021) and estimated the proportion of genetic variation that can be uniquely attributed to climate (the five climatic variables selected for genomic offset predictions; table S7), neutral population structure (first three axes of a PCA based on genomic data; fig. S3) and geography (distance-based Moran's eigenvector maps or geographical coordinates) using a combination of RDAs and partial RDAs (pRDAs) implemented in the *vegan* R package (Oksanen et al. 2022; see section 4 of the Supplementary Information).

2.6 Identification of SNPs potentially involved in climate adaptation

We identified SNPs covarying with climatic gradients using five gene-environment association methods (table 2): Redundancy Analysis (RDA), partial RDA (pRDA), Latent Factor Mixed Model (LFMM), BayPass and Gradient Forest (GF). These methods were chosen based on their different but complementary features (e.g., univariate vs multivariate, accounting or not for population genetic structure). Prior to such analyses, missing allelic values were imputed using the most common allele within the main gene pool of the genotype of concern (although we acknowledge that some genotypes had high admixture rates). Gene-environment associations were estimated based on the average climate over the period 1901-1950 at the location of the 34 studied populations to capture the climatic conditions under which the populations may have evolved.

RDA-based GEA approach is a multivariate constrained ordination method that models the linear associations among the climatic variables and genomic variation (Capblancq et al. 2018, Capblancq and Forester 2021). In the pRDA approach, the first three axes of a principal component analysis (PCA) based on centered and scaled population allele frequencies not filtered for minor allele frequencies (fig. S3) were added as conditioning variables to the RDA model to account for population genetic structure. Both in the RDA and pRDA, we identified outlier SNPs by first estimating the Mahalanobis distances between each locus and the center of the RDA space along the significant axes (Capblancq et al. 2018), and then selecting SNPs with extreme Mahalanobis distances based on a false discovery rate of 5%.

For LFMM, we used the new algorithm version available in the *LEA* R package, which

estimates locus-specific effect sizes by using a least-square method and incorporating multiple climatic variables (Gain and François 2021). Population genetic structure is accounted for with latent factors. As with RDA, outlier SNPs were identified based on a false discovery rate of 5%.

The standard covariate model from the BayPass software is an univariate approach in which the neutral genetic structure is accounted for using a population covariance matrix based on the population allele frequencies (Gautier 2015). SNPs were considered outliers if the median Bayes Factor (calculated over five independent runs) of their association with at least one climatic variable was higher than 10 deciban units, which corresponds to, at minimum, strong evidence on the Jeffrey's scale (Jeffreys 1961).

The GF method to identify outlier SNPs consists in fitting GF models individually to each SNP and calculating empirical p-values based on their $\mathcal{R}^2$ rank (Lotterhos and Whitlock 2014), as described in Fitzpatrick et al. (2021) and Capblancq et al. (2023). We ran three independent runs and selected the 0.5% SNPs with the lowest empirical p-values for each run (i.e., 49 SNPs). We then considered as outliers only those SNPs identified by the three runs.

For genomic offset predictions, we used three sets of candidate SNPs: all outlier SNPs (i.e., outlier SNPs identified by at least one gene-environment association method), common outlier SNPs (i.e., outlier SNPs identified by at least two methods) and outlier SNPs considering population structure correction (i.e., outlier SNPs identified by at least one method correcting for population genetic structure, namely BayPass, LFMM and pRDA). When some outlier SNPs were located on the same scaffold/contig (a scaffold/contig measuring

approximately between 400 and 10,000 bp), we kept the SNP with the lower p-value in the RDA. This decision aimed to reduce redundancy from SNPs in close proximity, ensuring that retained SNPs represent independent adaptation signals and preventing overrepresentation of specific genomic regions in the predictions. Among the loci that were not identified as outliers by any of the gene-environment association methods, we selected two sets of control SNPs with the same number of SNPs than the set with all candidate SNPs: randomly sampled SNPs and SNPs with similar allele frequencies than the candidate SNPs. Finally, we also used a sixth set of SNPs containing all 9,817 SNPs.

	RDA/pRDA	**GF**	**BayPass**	**LFMM**
Method name	(Partial) Redundancy Analysis	Gradient Forest	Generalized Dissimilarity Modeling	Latent Factor Mixed Model
Genomic input data	Population allele frequencies	Population allele frequencies	Population allele counts	Genotype allele counts
Response variable	Multivariate	Univariate	Univariate	Univariate
Predictors	Multivariate	Multivariate	Univariate	Multivariate
Linearity	Linear	Non-linear	Linear	Linear
Population structure correction	No correction (RDA) Correction with PC scores (pRDA)	No correction	Correction with a population covariance matrix (Ω)	Correction with latent factors
Metric to evaluate the SNPs	Mahalanobis distances between each locus and the center of the RDA space along the significant axes	Empirical p-values based on their $\mathcal{R}^2$ rank	Median Bayes Factors (BFs) calculated over 3 independent runs	Locus-specific effect sizes
Threshold to select the outlier SNPs	False discovery rate of 5%	0.5% of the SNPs with the lowest empirical p-values	Median Bayes factor across five runs $>$ 10 deciban units	False discovery rate of 5%
R packages and references	*vegan* R package v2.6.4 Oksanen et al. (2022) Capblancq et al. (2018) Capblancq and Forester (2021)	*gradientForest* R package Ellis et al. (2012) Lotterhos and Whitlock (2014) Capblancq et al. (2023) Fitzpatrick et al. (2021)	Gautier (2015) Jeffreys (1961)	*lea* R package v3.16.0 Caye et al. (2019) Frichot et al. (2013) Gain and François (2021)

Table 2: Gene-environment association (GEA) methods used for identifying the SNPs potentially involved in climate adaptation. Acronyms: PCs for principal components (see fig. S3), SNPs for single nucleotide polymorphisms.

2.7 Genomic offset predictions

	RDA/pRDA	GF	GDM	LFMM
Method name	(Partial) Redundancy Analysis	Gradient Forest	Generalized Dissimilarity Modeling	Latent Factor Mixed Model
Genomic input data	Population allele frequencies	Population allele frequencies	F_{ST} matrices	Genotype allele counts
Response variable	Multivariate	Univariate	Univariate	Multivariate
Predictors	Multivariate	Multivariate	Multivariate	Multivariate
Gene-climate relationships	Linear	Non-linear turnover functions	Non-linear I-splines	Linear
Population structure correction	No correction (RDA) Correction with PC scores (pRDA)	No correction	Correction with geographical distances	Correction with latent factors
R packages and references	*vegan* R package v2.6.4 Oksanen et al. (2022) Capblancq et al. (2018) Capblancq and Forester (2021)	*gradientForest* R package Ellis et al. (2012) Lotterhos and Whitlock (2014) Capblancq et al. (2023) Fitzpatrick et al. (2021)	*gdm* R package v1.5.0.9.1 Fitzpatrick et al. (2025) Ferrier et al. (2007) Fitzpatrick and Keller (2015)	*lea* R package v3.16.0 Caye et al. (2019) Frichot et al. (2013) Gain and François (2021)

Table 3: Genomic offset methods used for evaluating prediction consistency and empirical validity.

To address our first research question (Q1), we evaluated the consistency in genomic offset predictions under future climates at the location of the 34 studied populations across five methods, the six SNP sets and five general circulation models (table 1, first column). The five methods, namely GF, RDA, pRDA, LFMM and GDM (described in table 3), rely on common steps: (i) estimating gene-climate relationships under the reference period, (ii) projecting the genomic composition across the landscape under reference and future climates, and (iii) calculating the difference between the two genomic compositions for each pixel of the landscape, i.e., the genetic change required to maintain the estimated gene-climate relationships under future climates (Capblancq et al. 2020). We chose these methods because they are among those most commonly used, encompass both linear and nonlinear approaches, and account for population genetic structure in different ways (table 3). Genomic offset was initially predicted separately for each general circulation model to assess variability across models. Subsequently, the predictions from the five models were averaged to compute a

mean genomic offset.

2.8 Validation of genomic offset predictions

Direct estimation of the correlations between genomic offset predictions and the raw height and mortality data in the inventory plots and common gardens was not feasible due to the need to account for confounding factors affecting the phenotypes and the specificities of the experimental designs. The development and implementation of models designed to test the empirical validity of genomic offset predictions are described in the sections below.

2.8.1 In common gardens

We evaluated the empirical validity of genomic offset predictions in common gardens (research question Q2) by examining the association between genomic offset predictions and height and mortality data in the five common gardens from the CLONAPIN network. Genomic offset was predicted at the common garden locations, using the 1901-1950 climate at the location of the populations and the gene-climate relationships estimated in section 2.7 as reference, and the climatic conditions between the planting and the measurement dates at the location of the common gardens for the predictions (table 1, second column). These predictions are expected to capture climate maladaptation of the populations when transplanted into the new climates of the common gardens. Their association with height and mortality was also compared to that of the climatic transfer distances (section 2.4).

We modeled the probability of mortality p_p in the population p independently in the five common gardens as follows:

$$
\begin{aligned}
a_p &\sim \text{Binomial}(N_p, p_p) \\
\text{logit}(p_p) &= \beta_0 + \beta_H H_p + \beta_X X_p
\end{aligned}
\tag{1}
$$

a_p is the count of individuals that died in the population p. N_p is the total number of individuals from the population p that were initially planted in the common garden. X_p is the genomic offset or the climatic transfer distance of the population p, with β_X being its associated coefficient. H_p is a proxy of the initial tree height at the planting date (i.e., population intercept estimated across all common gardens in model 1 of Archambeau et al. 2022), with β_H being its associated regression coefficient. Initial height at planting was included in the models to account for the observed higher survival of taller trees in the common gardens. $\mathcal{N}(0, 5)$ prior distributions were used for β_0, β_H and β_X.

We modeled tree height independently in the five common gardens as follows:

$$
\begin{aligned}
Y_{ipb} &\sim \mathcal{N}(\mu_p, \sigma^2) \\
\mu_p &= B_b + \beta_{X1} X_p + \beta_{X2} X_p^2 + \beta_H H_p
\end{aligned}
\tag{2}
$$

Y_{ipb} is the height of the individual i in the population p and the block b. B_b are the block intercepts. σ^2 is the residual variance. β_{X1} and β_{X2} are the linear and quadratic regression coefficients of X_p, respectively, and β_H is the linear regression coefficient of H_p (see equation 1). The quadratic form was used to allow the slope of the association between height and the genomic offset (or the climatic transfer distance) to vary (such as in Fitzpatrick et al. 2021). $\mathcal{N}(0, 1)$ prior distributions were used for B_b, β_{X1}, β_{X2} and β_H and Exp(1) for σ.

2.8.2 In natural populations

We assessed the empirical validity of genomic offset predictions in natural populations (research question Q3) by examining the association between genomic offset predictions and mortality rates in the inventory plots. Genomic offset was predicted at the plot locations, using the 1901-1950 climate and the gene-climate relationships estimated in section 2.7 as reference and the climatic conditions during the inventory periods for the predictions (table 1, third column). These predictions are expected to reflect climate maladaptation occurring during the inventory periods (e.g., fig. 7b for genomic offset predictions with GF and all candidate SNPs). As for the common gardens, their association with mortality rates was also compared to that of the climatic distances (section 2.4).

We modeled the probability of mortality p_i of maritime pine in the plot i during the census interval Δ_i with a complementary log-log (cloglog) link. This function models the log cumulative hazard and is a standard approach in survival analysis for data with varying census intervals (e.g., Fortin et al. 2008).

$$\begin{aligned} m_i &\sim \text{Binomial}(N_i, p_i) \\ \log(-\log(1-p_i)) &= \beta_{0,c} + \beta_C C_i + \beta_{DBH} DBH_i + \beta_{C*DBH} C_i DBH_i + \beta_X X_i + \log(\Delta_i) \end{aligned} \tag{3}$$

N_i is the total number of maritime pines in the plot i. m_i is the number of maritime pines that died during the census interval Δ_i in the plot i (i.e., five years in the French plots and the variable number of years between two inventories in the Spanish plots). C_i is the basal area of all tree species found in the plot i (to account for the competition-related mortality), with

β_C being its associated regression coefficient. DBH_i is the mean diameter at breast height of all maritime pines in the plot i (to account for age-related mortality), with β_{DBH} being its associated regression coefficient and β_{C*DBH} being the regression coefficient capturing the interaction between C_i and DBH_i. X_i is the genomic offset or climatic distance predicted in the plot i, with β_X being its associated regression coefficient. $\beta_{0,c}$ are country-specific intercepts that account for the methodological differences between the French and Spanish inventories. $\mathcal{N}(0,1)$ prior distributions were used for $\beta_{0,c}$, β_C, β_{DBH}, β_{C*DBH} and β_X.

2.8.3 Model implementation and evaluation metrics

For mortality models, the predictive ability of the variables of interest (i.e., genomic offset predictions and climatic distances) was evaluated based on the strength and sign of their regression coefficients (β_X in equations 1 and 3). We expected these coefficients to be positive, indicating that populations with higher genomic offset or climatic distances are more likely to be climatically maladapted and, therefore, should experience higher mortality rates. We also ensured that these coefficients were statistically unlikely to occur by chance. Given the limited predictive power of genomic data on trait variation in non-model species such as forest trees, our primary goal was to detect associations rather than to achieve high predictive accuracy.

For height models, the predictive ability of the variables of interest was assessed using β_{X_1} and β_{X_2} regression coefficients in equation 2 and by comparing the proportion of variance explained ($\mathcal{R}^2$) with that of models that did not include the variables of interest. This approach enabled us to identify and exclude genomic offset predictions that displayed unexpected quadratic relationships (e.g., U-shaped associations), while retaining those that

showed a consistent monotonic negative association with height (i.e., the more climatically maladapted a population is, the less it should grow).

As an alternative to regression coefficients, we estimated Pearson and Spearman correlations between genomic offset predictions (or climatic distances) and height and mortality rates corrected for confounding factors, both in the common gardens and the inventory plots. To do this, we predicted height and mortality using only the confounding factors (applying the models described above but excluding genomic offsets or climatic distances). We then extracted the model residuals and estimated their correlations with genomic offset predictions. However, we consider this two-step approach less robust than the models described earlier as it does not propagate the uncertainty in parameter estimation and cannot account for potential quadratic associations in height models. For these reasons, we only report these correlations in the Supplementary Information.

The statistical models of the validation steps were implemented in a Bayesian framework using the Stan probabilistic programming language based on the no-U-turn sampler algorithm (Carpenter et al. 2017), and executed in R with the *rstan* package (Guo et al. 2025). Weakly informative priors were used to statistically regularize the parameters and thus avoid getting aberrant values (Lemoine 2019). All analyses were undertaken using R Statistical Software v4.2.2 (R Core Team 2022). Scripts and Stan code of the models are available at https://doi.org/10.5061/dryad.bnzs7h4jt.

3 Results

Based on RDA/pRDA approaches, geography, climate and neutral population genetic structure explained 80.3% of the variation in population-allele frequencies (table S8). Single variables explained 29.8% of the variance (7.9% by climate, 8.3% by geography and 13.6% by population genetic structure) while the rest (50.5%) could not be uniquely attributed to a given variable (i.e., confounded effects).

Gene-environment association methods identified 482 outlier SNPs: 240 with the RDA, 178 with the pRDA, 46 with BayPass, 40 with GF and 120 with LFMM (fig. 3a). 85 SNPs were identified by at least two methods and 277 SNPs were identified by at least one method correcting for population structure. After retaining a single outlier SNP from those located on the same scaffold/contig, we ended up with 380 candidate SNPs identified by at least one method, 69 candidate SNPs identified by at least two methods and 221 candidate SNPs identified by at least one method correcting for population genetic structure. When mapped to the reference genome of a related species (*Pinus tabuliformis*; Niu et al. 2022), outlier SNPs were found to be present on all chromosomes, with clusters observed on chromosomes 2 and 7 (fig. 3b and table S9). The number of SNPs with predictive power in GF models is given in table S10.

3.1 Variability in genomic offset predictions under future climates

We observed substantial variability in genomic offset predictions under future climates across methods, SNP sets, and general circulation models. The correlation coefficients

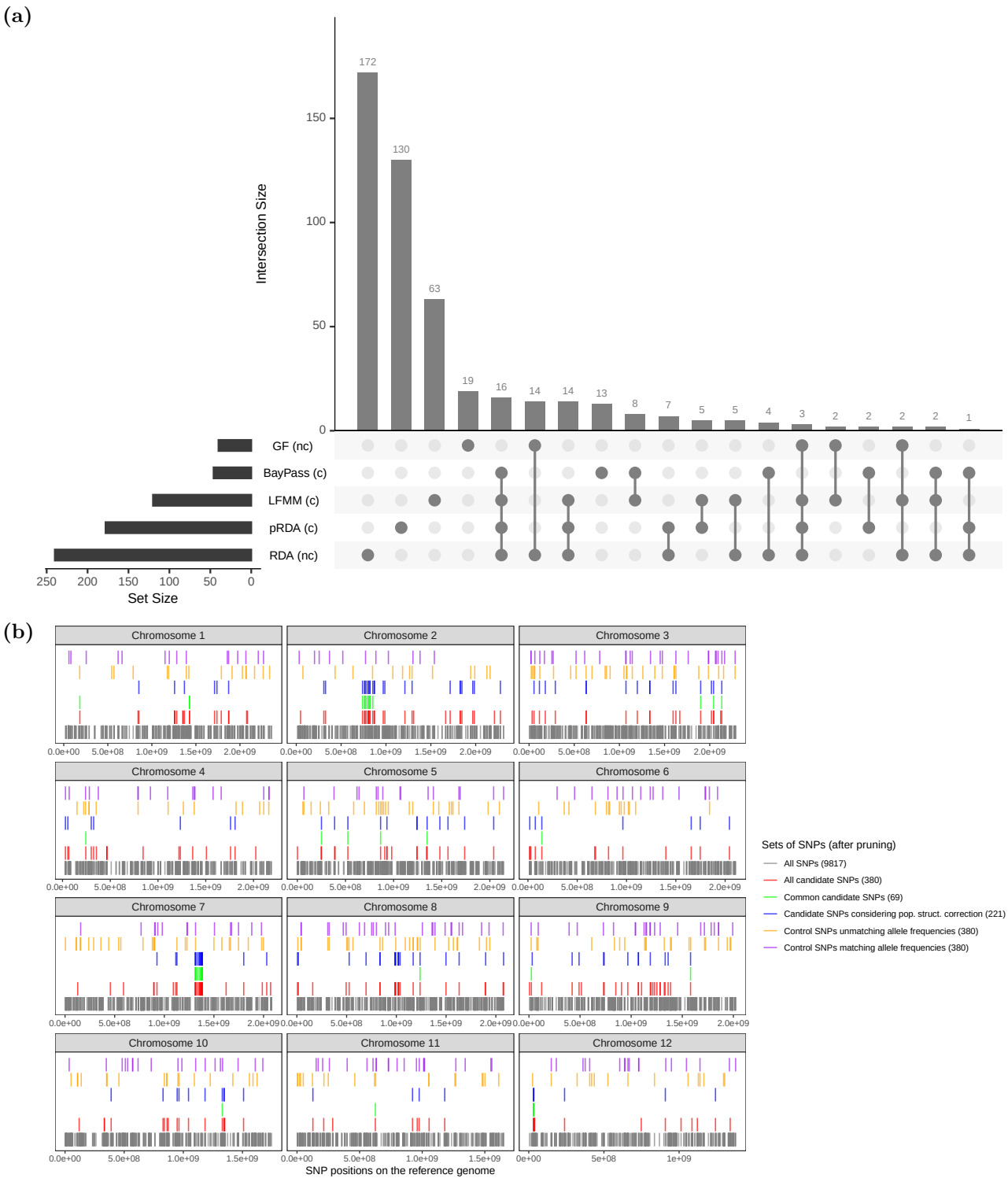

Figure 3: (a) Upset plot showing the number of outlier SNPs identified by each of the five gene-environment association (GEA) methods, namely Gradient Forest (GF), BayPass, Latent Factor Mixed Model (LFMM), Redundancy Analysis (RDA) and partial RDA (pRDA). Approaches annotated with '(c)' incorporate correction for population structure, while approaches annotated with '(nc)' do not. (b) SNP positions on the chromosome-scale reference genome of a related species (i.e., *Pinus tabuliformis*; Niu et al. 2022), as such a reference is not yet available for maritime pine. The number of SNPs mapped on each chromosome (and on unassembled contigs) is presented in table S9.

reported in this section were calculated using predictions averaged across the five general circulation models, with fig. 4 illustrating only the variability in predictions derived from two SNP sets (all SNPs and all candidate SNPs). Visualizations that explore the full range of combinations of SNP sets, methods, and general circulation models, as well as their relationship with climatic distances, can be accessed via a Shiny app at https://juliettearchambeau.shinyapps.io/GenomicOffsetPredictionVariabilityInMaritimePine/. We verified that the imputation of missing data did not introduce biases in genomic offset predictions by predicting the genomic offset using SNPs without any missing data (3,258 SNPs). Since these predictions were highly correlated with those based on all SNPs (results available in the Shiny app), they were not included in the subsequent validation analyses.

Variability among SNP sets. Predictions from LFMM and pRDA showed moderate to strong correlations across SNP sets ($0.44 \leq \rho \leq 0.97$ for pRDA and $0.85 \leq \rho \leq 1$ for LFMM). In contrast, GF predictions based on the set of common candidate SNPs diverged from those derived from other SNP sets (except for the set of all candidate SNPs; $\rho = 0.9$), while predictions among the remaining SNP sets were strongly correlated ($0.49 \leq \rho \leq 0.99$). For RDA, predictions based on the candidate SNPs corrected for population structure and the common candidate SNPs were uncorrelated with predictions from other SNP sets, which were otherwise strongly correlated with one another. GDM was the most sensitive to SNP set choice: predictions from control SNP sets were highly correlated among themselves, predictions for the common candidate SNPs were moderately correlated with those from the set of all candidate SNPs ($\rho = 0.74$), while correlations among the other SNP sets were weak or negative.

Variability among methods. Predictions from LFMM and pRDA were generally positively

correlated ($\rho \geq 0.61$; fig. 4). GF predictions showed moderate correlations with those of pRDA and LFMM ($0.59 \leq \rho \leq 0.77$), except for the predictions based on all candidate SNPs ($0.20 \leq \rho \leq 0.33$) and the common candidate SNPs ($-0.12 \leq \rho \leq 0.11$). Predictions from GDM and RDA were generally weakly or not correlated with predictions from other methods. GDM predictions based on the common candidate SNPs, and to a lesser extent all SNPs, were even negatively correlated with predictions from other methods. However, there were a few exceptions where predictions from GDM and RDA were correlated with those from other methods: predictions based on the candidate SNPs corrected for population structure for both RDA and GDM, predictions based on all SNPs for GDM, and predictions based on common candidate SNPs for RDA.

Variability among methods for specific SNP sets. For all candidate SNPs, only LFMM and pRDA predictions were strongly positively correlated ($\rho = 0.89$; fig. 4). Predictions based on common candidate SNPs were correlated among pRDA, RDA, and LFMM ($0.73 \leq \rho \leq 0.95$), but not for GF and GDM ($-0.53 \leq \rho \leq 0.33$). For candidate SNPs corrected for population structure, predictions were generally positively correlated across methods ($0.50 \leq \rho \leq 0.94$). For control SNP sets, both with unmatched or matched allele frequency, GF, pRDA, and LFMM predictions were positively correlated ($0.60 \leq \rho \leq 0.81$), but not RDA and GDM predictions ($-0.59 \leq \rho \leq 0.47$). For all SNPs, predictions were moderately positively correlated ($0.38 \leq \rho \leq 0.68$), except for RDA ($-0.37 \leq \rho \leq 0.14$).

Variability across general circulation models. This source of variability was noticeable but generally lower than the variability among methods and SNP sets. Some methods demonstrated greater consistency across general circulation models, e.g., GF and LFMM, while pRDA and RDA showed higher inconsistency.

Associations between genomic offset predictions and Euclidean climatic distances. LFMM showed the strongest associations with Euclidean climatic distances, particularly for predictions using the three sets of control SNPs (figs. S4-S9). pRDA predictions, GDM predictions for the candidate SNPs corrected for population structure and GF predictions for the three control SNP sets and the candidate SNPs corrected for population structure exhibited modest correlations with Euclidean climatic distances (figs. S4-S9). Other genomic offset predictions displayed weak or no associations with Euclidean climatic distances, with some even showing negative correlations for GDM and the uncorrected candidate SNPs (figs. S4-S9).

3.2 Validation of genomic offset predictions in common gardens

3.2.1 Mortality models

In the three common gardens with dry and hot summers (Cáceres, Fundão and Madrid), lower initial tree height proxy (H_p; the population height intercepts estimated across all common gardens) was associated with higher mortality rates (fig. S10). Genomic offset predictions had regression coefficients that were all in the expected direction (i.e., positive association with mortality rates), except for pRDA predictions with common candidate SNPs in Cáceres (fig. 5). Most coefficients did not have 95% credible intervals overlapping zero.

In Bordeaux, positive regression coefficients that did not overlap zero were obtained for GDM and GF predictions, LFMM predictions with uncorrected candidate SNPs, and RDA predictions with all candidate SNPs (fig. 5). To give an example of the effect size, a one-standard deviation increase in GDM genomic offset predictions with control frequency-matched SNPs corresponded to an estimated mean increase in tree mortality probability of

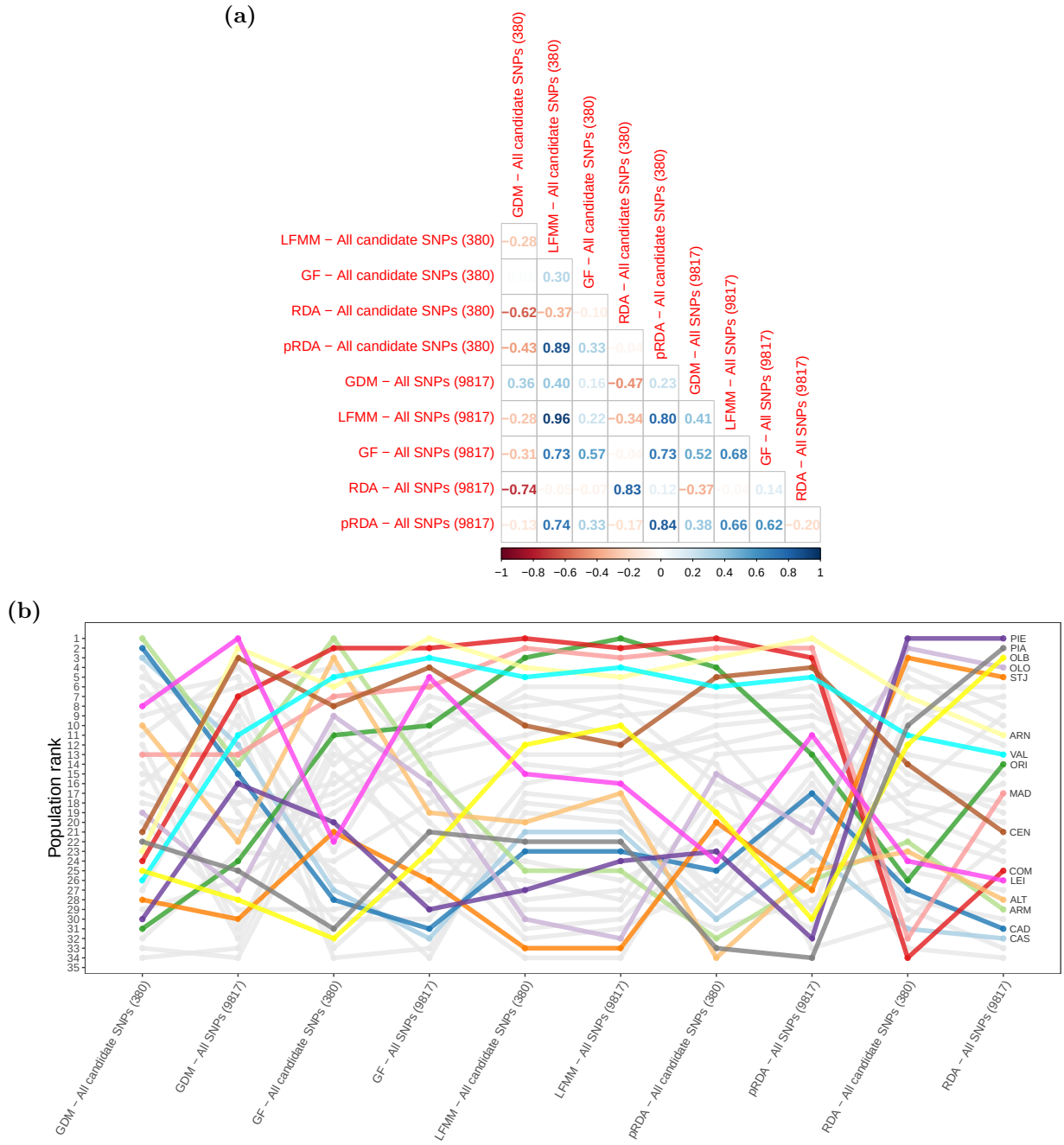

Figure 4: Variability in genomic offset predictions under future climates across the five methods tested (GDM, GF, LFMM, pRDA and RDA) and two SNP sets (all SNPs, i.e., 9,817 SNPs, and all candidate SNPs, i.e., 380 SNPs). Genomic offsets were predicted for the 34 studied populations in the common gardens, using climatic data from 1901–1950 as the reference period and projections for 2041–2060 under SSP 3.7-0 and five general circulation models for the prediction period (see section 2.7 and table 1, first column). Predictions were generated separately for each general circulation model and subsequently averaged by population. The variability in genomic offset predictions, considering all combinations of SNP sets, methods, and general circulation models, along with their relationships to climatic distances, can be visualized via a Shiny app at https://juliettearchambeau.shinyapps.io/GenomicOffsetPredictionVariabilityInMaritimePine/. (a) Pairwise Pearson correlations between genomic offset predictions. (b) Population ranks based on the genomic offset predictions, where populations with higher genomic offset have lower rank values. Colored populations are those with genomic offset ranks in the top three lowest positions (i.e., highest genomic offset values) in at least one column, where each column represents a combination of SNP set and method.

30.5% in Bordeaux. In Asturias, no positive association between genomic offset predictions and mortality rates was observed (fig. 5). In these last two common gardens, which are under a milder Atlantic climate, the initial tree height proxy was not, or barely, associated with mortality rates (fig. S10).

Correlations (both Spearman and Pearson) between corrected mortality rates and genomic offset predictions aligned closely with regression coefficients, with significant correlations mainly observed in Madrid and Fundão (figs. S11, S12).

Climatic transfer distances based on the six climatic variables (i.e., Euclidean distances) or on temperature seasonality (*bio4*) were positively associated with mortality rates in the dry common gardens, though their credible intervals overlapped zero in Cáceres (fig. 5). Those based on temperature seasonality were also positively associated with mortality rates in Bordeaux (fig. 5). Climatic transfer distances based on the other climatic variables did not show consistent positive associations with mortality rates across the common gardens (fig. 5).

3.2.2 Height models

As expected, tree height in the five common gardens was strongly associated with the proxy for initial tree height (fig. S13). For genomic offset predictions and climatic transfer distances, we expected their β_{X_1} regression coefficients to be negative (i.e., populations with higher genomic offset grow less) and their β_{X_2} coefficients to be small (i.e., height decreases monotonically with increasing genomic offset predictions). However, very few combinations of methods and SNP sets exhibited these patterns, and no consistency across methods or

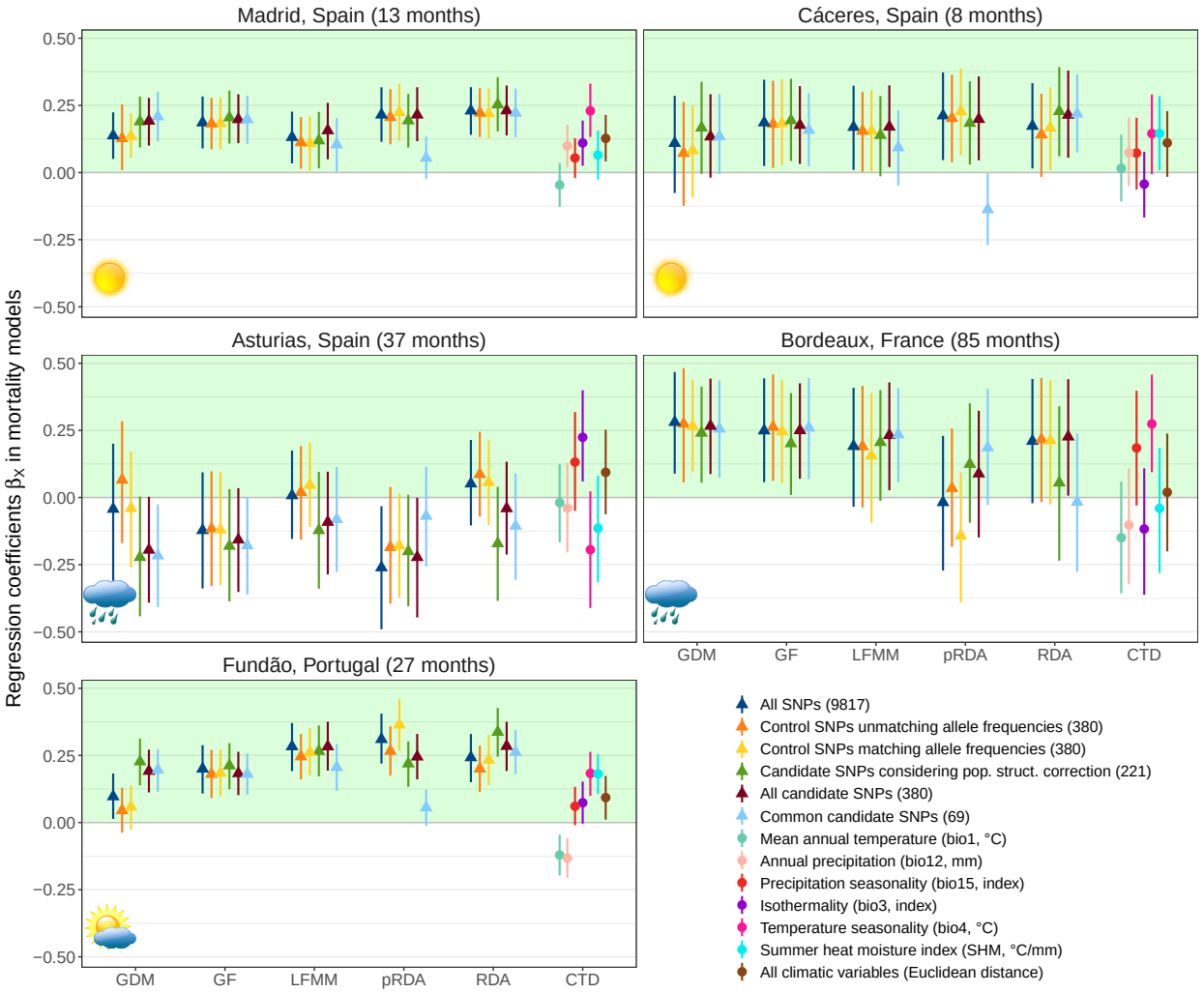

Figure 5: Estimated means and 95% credible intervals of the regression coefficients β_X standing for the association between mortality rates and genomic offset predictions or climatic transfer distances in the five common gardens. Graph titles include the time in months corresponding to the age at which survival was recorded. Genomic offsets were predicted using climatic data from 1901 to 1950 at the location of the 34 populations for the reference period, and from the planting date to the measurement date at the location of the common gardens for the prediction period (see section 2.8.1 and table 1, second column). Coefficients in the green area have the expected sign, reflecting higher mortality rates in populations with higher genomic offset predictions or climatic transfer distances. The weather icons represent the climatic conditions in the five common gardens between the planting and measurement dates: Atlantic climates with mild winters and relatively wet summers in Asturias and Bordeaux, Mediterranean climates with severe summer droughts in Cáceres and Madrid, and intermediate climates with wet winters but dry summers in Fundão.

SNP sets was observed (see expected associations in fig. 6). Moreover, the proportion of variance explained by height models including genomic offset predictions or climatic transfer distances was nearly identical to that explained by models without these predictors (fig. S14). Similar results for the correlations between corrected height and genomic offset predictions can be found in figs. S15, S16.

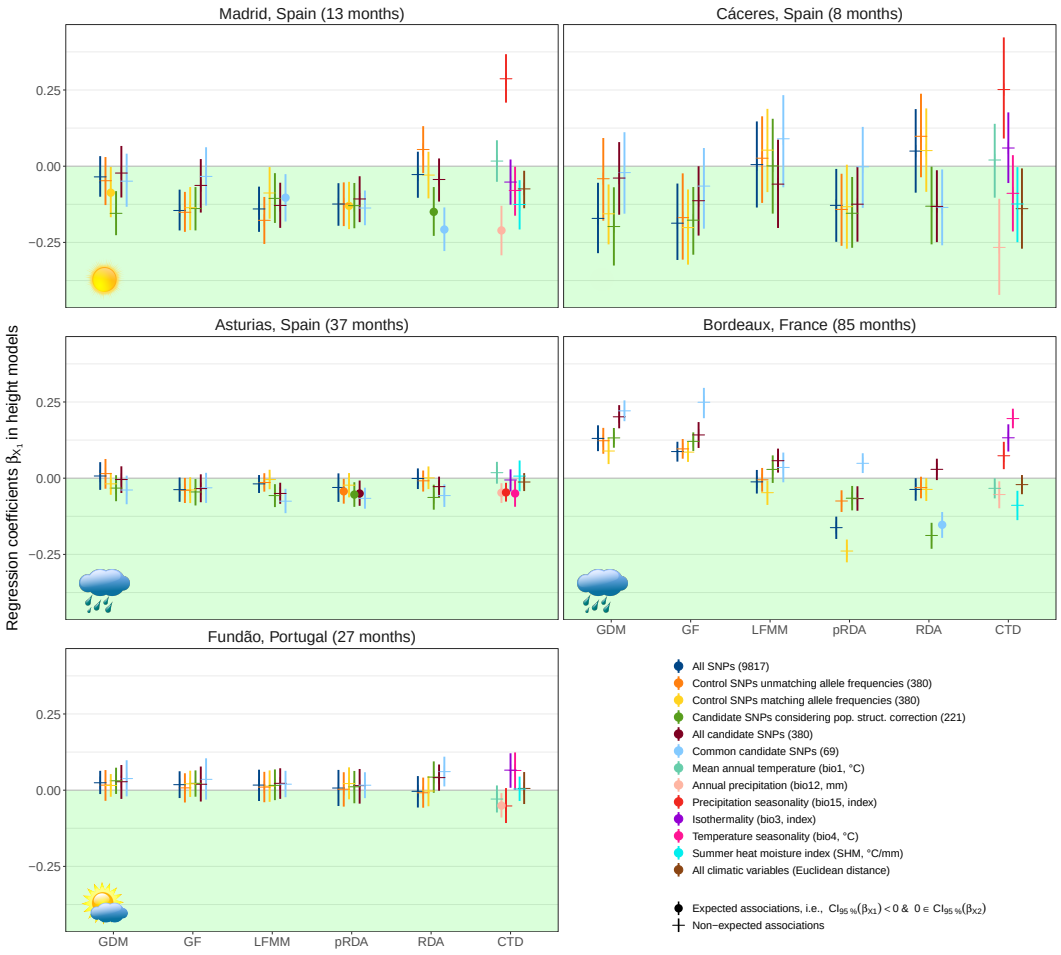

Figure 6: Estimated means and 95% credible intervals of the regression coefficients β_{X_1} standing for the association between height and genomic offset predictions or climatic transfer distances in the five common gardens. Expected associations are those in which the 95% credible interval of β_{X_1} is negative (i.e., populations with higher genomic offset or climatic transfer distances grow less; illustrated by the green areas on the plot) and the 95% credible interval of β_{X_2} encompasses zero, suggesting a monotonic decrease in height with increasing genomic offset predictions (i.e., the higher the genomic offset of a population, the less it is expected to grow). Graph titles include the time in months corresponding to the age at which height was recorded. Genomic offsets were predicted using climatic data from 1901 to 1950 at the location of the 34 populations for the reference period, and from the planting date to the measurement date at the location of the common gardens for the prediction period (see section 2.8.1 and table 1, second column). The weather icons represent the climatic conditions in the five common gardens between the planting and measurement dates: Atlantic climates with mild winters and relatively wet summers in Asturias and Bordeaux, Mediterranean climates with severe summer droughts in Cáceres and Madrid, and intermediate climates with wet winters but dry summers in Fundão.

3.3 Validation of genomic offset predictions in natural populations

In the inventory plots, mortality rates were positively associated with basal area of all tree species found in each plot (fig. S17) and the mean DBH of maritime pines in each plot (fig. S18), while their interaction showed a negative association (fig. S19). Mortality rates were positively associated (i.e., expected direction) with the genomic offset predictions

based on RDA and pRDA (except for pRDA predictions with control frequency-matched SNPs), but were negatively associated with predictions based on GF and GDM (except for GDM predictions with all candidate SNPs; fig. 7c). The regression coefficients associated with RDA and pRDA predictions were highly unlikely to occur by chance (fig. S20). The strongest association was observed for RDA and all candidate SNPs, where a one-standard deviation increase in genomic offset predictions corresponded to an estimated mean increase in tree mortality probability of 59.8% in Spain and 63.3% in France. In fig. 7, we also illustrate how higher genomic offset predictions based on RDA and all candidate SNPs (mostly observed in southwestern France; fig. 7b) translate into higher predictions of annual probability of tree mortality in the inventory plots (when the other covariates of the validation models are fixed to the mean and the country fixed to Spain; fig. 7d). Regarding climatic distances, annual precipitation (*bio12*) and isothermality (*bio3*) showed positive coefficients nearly as strong as the strongest coefficients from genomic offset predictions, while the other climatic distances showed null or negative regression coefficients (fig. 7c). Last, Spearman and Pearson correlations between corrected mortality rates and genomic offset predictions closely aligned with regression coefficients (figs. S21, S22).

4 Discussion

The genomic offset concept has gained considerable traction in recent years, and is often suggested as a tool for predicting population performance under climate change *in situ* or

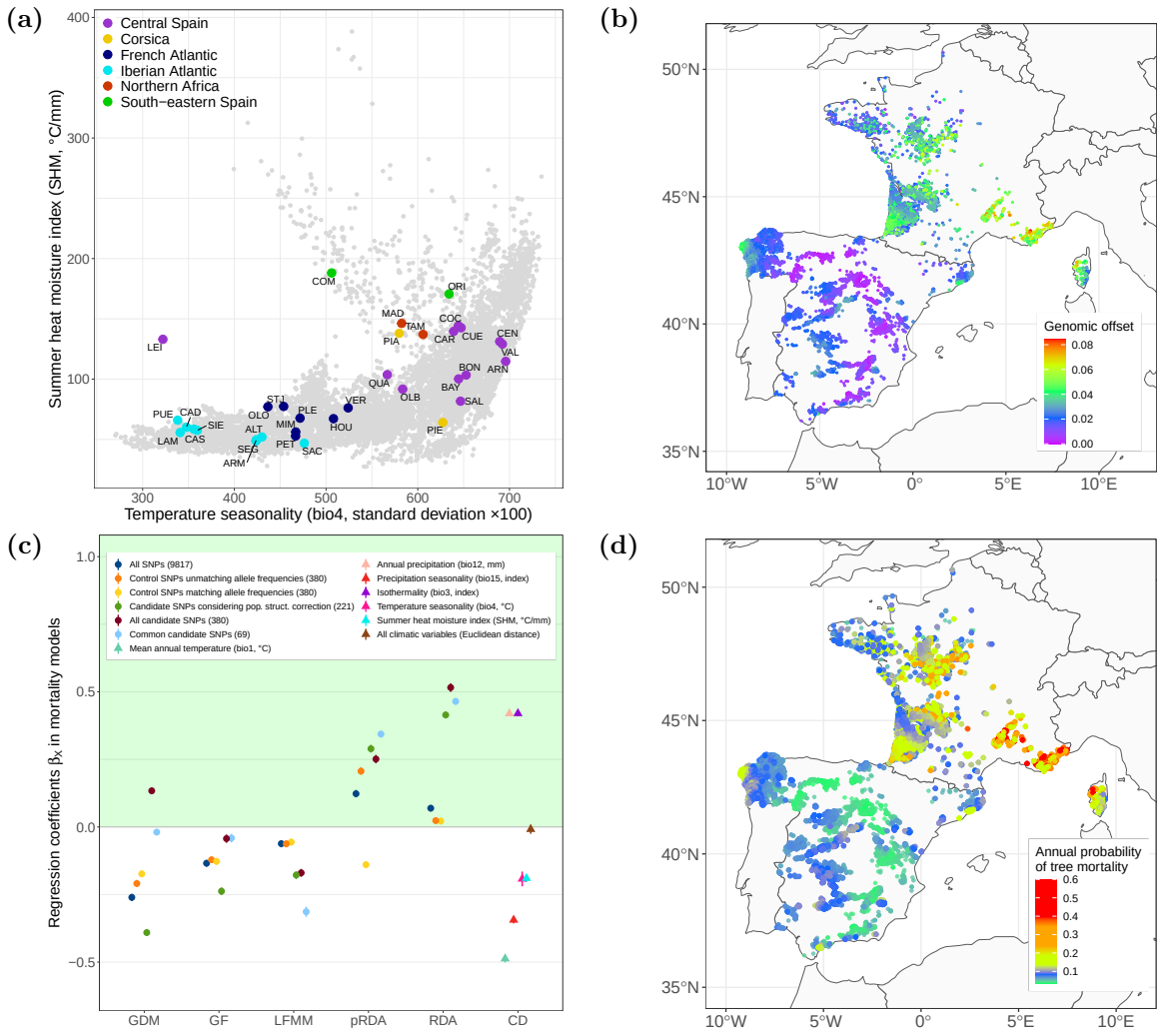

Figure 7: Validation of genomic offset predictions using mortality data from the French and Spanish national forest inventory (NFI) plots. (a) Summer heat moisture (SHM) index and temperature seasonality (two strong predictors of the RDA models with all candidate SNPs) at the plot locations (in gray) and the 34 sampled populations (coloured according to their main gene pool). Climatic values correspond to average climates over the reference period 1901-1950. (b) Genomic offset predictions with RDA and all candidate SNPs at the locations of the inventory plots. These predictions capture the mismatch between the projected current genomic composition of the populations and the genomic composition predicted to be optimal under the climatic conditions of the inventory period. (c) Estimated means and 95% credible intervals of the regression coefficients β_X standing for the association between mortality rates and genomic offset predictions or climatic distances in the inventory plots. Coefficients in the green area have the expected sign, indicating that plots with higher genomic offset or climatic distance also have higher mortality rates. (d) Predicted annual probability of mortality in each inventory plot using genomic offset predictions from RDA and all candidate SNPs, with covariates C (basal area of all tree species) and DBH (mean DBH of all maritime pines) fixed to the mean and country fixed for Spain.

at a potential location for transplantation (e.g., Rhoné et al. 2020, Lachmuth et al. 2023). However, genomic offset predictions have only been validated under a limited number of scenarios (mostly local-foreign fitness offsets estimated from height measurements in common gardens; e.g., Fitzpatrick et al. 2021) and species, e.g., balsam poplar (*Populus balsamifera*) in Fitzpatrick et al. (2021) and lodgepole pine (*Pinus contorta*) in Capblancq et al. (2018). Using data from 34 populations (454 genotypes) of maritime pine, a forest tree species with strong population genetic structure, we observed high variability across genomic offset predictions from five methods (GF, GDM, LFMM, RDA and pRDA), six sets of loci (control and candidate SNPs) and five general circulation models. Genomic offset predictions were generally validated against mortality data from common gardens; however, no single method or SNP set consistently outperformed the others. More pronounced differences in predictive ability were found for mortality in natural populations (home-away fitness offsets), with RDA and pRDA using candidate SNPs showing higher predictive performance compared to other combinations. Conversely, we found limited evidence of the expected monotonic negative associations between genomic offset predictions and tree height in common gardens, which we attribute to the strong effect of population genetic structure on tree height in maritime pine (Archambeau et al. 2022). Our study demonstrates the current risks of relying on predictions from a single method and highlights the challenges associated with implementing appropriate empirical validation approaches (Lotterhos and Whitlock 2014), as well as the potential value of incorporating observational data from natural populations in such validations. Further improvements in both the estimation and validation of genomic offset appear essential before these predictions can be reliably used as informative metrics in conservation or management strategies.

4.1 High variability in genomic offset predictions

Variability in genomic offset predictions across methods was somehow expected given their different theoretical assumptions for estimating gene-climate relationships (Gain et al. 2023). RDA/pRDA and LFMM assume linear adaptive gradients and Gaussian selection within populations (Capblancq and Forester 2021, Gain and François 2021), and under some conditions, Gain et al. (2023) demonstrated that their predictions should be identical. GF and GDM are nonparametric approaches that make no a priori assumption about the shape of the gene-climate relationships and the selection gradient within populations (Fitzpatrick and Keller 2015, Gain et al. 2023). While it is expected that differing methodologies produce varying predictions to some extent, the substantial variability observed across genomic offset predictions—spanning methods, SNP sets, and general circulation models—is concerning. Correlations among genomic offset predictions range from strongly negative to strongly positive, with many showing negligible correlations. Some populations that exhibit high genomic offset with certain methods (e.g., the ALT and CAD populations when using GDM with all candidate SNPs) display low genomic offset with other methods (e.g., RDA with all SNPs). This variability highlights a critical issue: conclusions about the risk of maladaptation can vary dramatically depending on the combination of methods and SNP sets chosen, making it difficult to draw robust, consistent conclusions.

Demonstrating the high variability in genomic offset predictions across methods is not new. Fitzpatrick and Keller (2015) pointed out the differences between GF and GDM predictions in the paper that launched the genomic offset concept and advised the use of the two approaches in tandem. Lind et al. (2024) found high variability among predictions from GF and RDA in Douglas fir (*Pseudotsuga menziesii*), but not in jack pine (*Pinus banksiana*).

Our results therefore provide further evidence that relying on the predictions of a single method without any knowledge of its empirical validity for the species under study must be avoided.

4.2 The role of population genetic structure

To date, no consensus has been reached on how to account for population genetic structure and demographic history in landscape genomics. This also applies to genomic offset approaches in which the first step is to identify a set of loci potentially involved in climate adaptation (Capblancq et al. 2023, Eckert and Neale 2023). In species for which climatic gradients that drive local adaptation covary with neutral genetic variation, correcting for population structure in gene-environment association methods reduces the number of false positives but at the expense of a higher number of false negatives (Lotterhos and Whitlock 2015). In red spruce, a species in which climate adaptation strongly covaries with neutral population structure and geographic distance, Capblancq et al. (2023) showed that there was almost no overlap among outliers identified by gene-environment association methods correcting for population genetic structure and those that did not, and that selecting outliers only from those methods that did correct resulted in the removal of most of the adaptive signal. Therefore, to obtain a set of candidate SNPs representative of climate adaptation, Capblancq et al. (2023) originally used a combination of four methods, two with correction for population structure and two without, and considered as candidates for local adaptation loci that were identified by at least two of them. This approach seemed appropriate for our study given the highly confounded patterns of population genetic structure and climate adaptation in our sampled populations, and more generally in maritime pine (Alberto et al.

2013, Jaramillo-Correa et al. 2015, Archambeau et al. 2022). However, only 69 outliers were detected by at least two gene-environment association methods (after filtering for nearby loci on the genome; fig. 3a), which is likely insufficient to capture the complex signal of climate adaptation. For this reason, we also retained a broader set of 380 candidate SNPs (205 of which were detected exclusively by methods that did not correct for population genetic structure), and another set of 221 SNPs identified by at least one method that did account for population structure (fig. 3a). Interestingly, genomic offset predictions based on RDA and pRDA using each of these three candidate SNP sets showed similar positive associations with mortality rates in the inventory plots, which were stronger than those based on control SNPs. This result suggests that the candidate SNP sets likely included loci located within or near genes involved in climate adaptation. Moreover, it indicates that most of the adaptive signal was already captured within the reduced sets of 69 common candidates and 221 candidates with population structure correction; however, this should be nuanced by the weaker associations with mortality rates observed in some of the common gardens for these smaller SNP sets, compared to those obtained with all candidates. These findings highlight the potential relevance of pre-selecting candidate SNPs, at least in the case of maritime pine. Still, this interpretation should be approached with caution, as these patterns were not observed when using GDM or GF.

The second step at which population genetic structure can impact genomic offset predictions is when estimating gene-climate relationships for the selected SNPs and then predicting genomic offset at the locations of interest. We used GF without correction for population genetic structure as it has been successfully validated with simulations (Láruson et al. 2022) and common garden data (Lind et al. 2024). Correcting GF turnover functions for popu-

lation genetic structure has been explored with Moran's eigenvector maps (Fitzpatrick and Keller 2015) or allele frequencies corrected for population relatedness based on the population covariance matrix (Fitzpatrick et al. 2021). However, the first approach still lacks empirical validation, while the second has only been validated in core populations of balsam poplar with low genetic structure. GDM was performed with correction for population genetic structure to estimate the gene-climate relationships (using population geographic coordinates) and no correction in the prediction model, whereas we applied the RDA without correcting for population structure at either stage. Last, LFMM and pRDA incorporated population genetic structure both in the estimation of the gene-climate relationships and in the prediction model (Rellstab et al. 2021), which likely explains the higher correlation among their predictions compared to the other methods. The validation steps did not allow us to discriminate between methods that correct for population genetic structure and those that do not, as all performed similarly well in the common gardens (based on mortality rates), and the two methods showing expected positive associations with mortality in inventory plots included one that corrected for population structure (pRDA) and one that did not (RDA).

Most importantly, our study has revealed the major effect that population genetic structure can have on the validation of genomic offset predictions in common gardens. Previous height growth models fitted on the five CLONAPIN common gardens showed that the genetic-by-environment interaction (G*E) explained very little variance, and that the genetic component of height growth was mainly explained by the gene pools of origin (Archambeau et al. 2022). In our study, we used the population intercepts across the five common gardens from the models of Archambeau et al. (2022) to account for the effect of the neutral genetic

structure (and therefore indirectly the initial tree height at the planting date) in the mortality and height models. In mortality models, most detected associations were in the expected direction when accounting for population genetic structure, which was not the case when this factor was omitted (results not shown). In contrast, for height models, we almost never observed the expected monotonic negative associations between genomic offset predictions and height across the five common gardens, but many negative associations with an inverse U-shaped pattern. This suggests that either there is no detectable climate maladaptation in height variation in maritime pine, or that climate adaptation is too strongly correlated with population genetic structure to be disentangled using our statistical models, or that maritime pine populations are currently not optimally adapted for this trait along climatic gradients, thus violating genomic offset theoretical assumptions and biasing its predictions. Consequently, height may not be a reliable fitness proxy in climate adaptation studies on maritime pine.

4.3 Validation of genomic offset predictions using different data sources

Our results first demonstrate the value of combining different traits (mortality and height in our study) to validate genomic offset predictions. Genomic offset predictions have mainly been validated with height data from common gardens until now (e.g., Capblancq et al. 2018, Fitzpatrick et al. 2021). However, our study suggests that using tree height to validate genomic offset predictions may not be appropriate in species with strong population genetic structure and low G*E, and that mortality data are probably more reliable. Greater relia-

bility of mortality relative to height (and DBH) for validating genomic offset predictions has also been found in jack pine (Lind et al. 2024). When both mortality and height data are available, an alternative option would be to estimate the association between height and genomic offset predictions, setting the height of dead individuals to zero, as done in Capblancq et al. (2023).

Second, robust validation of genomic offset predictions may considerably benefit from using different data sources, enabling the evaluation of different types of fitness offsets (Lotterhos 2024a). By combining large-scale observational data (to estimate home-away fitness offsets) with common garden data (to estimate local-foreign fitness offsets), we were able to highlight that good performance in local-foreign fitness offsets does not necessarily translate into good performance in home-away fitness offsets, as raised by Lotterhos (2024a). Indeed, while genomic offset methods performed nearly equally well in the common gardens, they showed discrepancies in validation when using mortality rates in the inventory plots. Moreover, estimating home-away fitness offsets derived from mortality rates in the inventory plots highlighted the greater empirical validity of candidate SNPs compared to control SNPs for RDA and pRDA (the two validated methods)—a discrepancy not observed with local-foreign fitness offsets from the common gardens (as also shown in Lind et al. 2024, Lind and Lotterhos 2025). To our knowledge, differences in the empirical validity of genomic offset predictions from candidate or control SNPs have not been demonstrated so far, although predicting genomic offset from a set of candidate SNPs is generally advised (Fitzpatrick and Keller 2015, Fitzpatrick et al. 2018, Capblancq et al. 2020).

Furthermore, empirical evidence linking genomic offset predictions to mortality rates in natural settings would offer insights not available from common gardens. For instance,

mortality events due to climate change, particularly drought-induced mortality, have increasingly been documented in maritime pine populations across the Mediterranean region (Gea-Izquierdo et al. 2019, Valeriano et al. 2021, Calama et al. 2024). If genomic offset predictions can identify populations at risk of such mortality, it would demonstrate the potential for these predictions to be applied directly to real-world forest management. Moreover, these predictions may provide insights into the evolutionary dynamics that may be at play in a natural setting. On the one hand, higher mortality rates have the potential to accelerate adaptive evolution by enhancing turnover within populations (Kuparinen et al. 2010). On the other hand, higher predicted genomic offset in populations with higher mortality rates suggests that these populations would have to undergo more significant changes to remain adapted to the changing climatic conditions, therefore counterbalancing the positive effects of mortality rates on adaptive evolution.

Despite these potential insights, care should be taken when interpreting this validation approach. First, although we corrected for some potential confounding factors (competition among trees, different sampling schemes across countries and differences in mean tree age across plots), we cannot assert that the remaining mortality events were caused by climate change alone. Indeed, mortality is a multifactorial stochastic process which is hard to model and whose causes are difficult to determine (Franklin et al. 1987, Lines et al. 2010), and inventory data are inherently noisy. However, this inherent messiness reflects the complexity of forest ecosystems, and previous studies using the same inventory data (e.g., Archambeau et al. 2020, for Scots pine and beech; and Changenet et al. 2021, for multiple species) have shown that drought-induced mortality patterns can indeed be detected. Second, predicting the genomic offset at the locations of the inventory plots relies on projecting the genomic

composition of the sampled populations across the landscape based on their estimated gene-climate relationships. Although our population sample represents the climatic space of the inventory plots relatively well (except for locations with high *SHM* or low *bio15*, *bio3* and *bio1*; figs. 7a, S23, S24), this step remains a spatial extrapolation, based on the assumption that the gene-climate relationships estimated in the studied populations hold true across the entire area covered by the inventory plots (Rellstab et al. 2021, Lind et al. 2024). These projections are particularly uncertain for the pRDA, as we had to attribute population genetic structure values for the inventory plots by assigning the principal component values of the closest populations, a crude approximation.

Finally, a better understanding of the conditions under which genomic offset predictions are valid would greatly benefit from the use of other data sources, such as experiments specifically designed to assess the ability of populations to grow outside their range (e.g., the REINFFORCE arboretum network; https://reinfforce2.plantedforests.org/), or regeneration and reproduction data in natural stands, and from the comparison of genomic offset predictions with predictions from other types of models such as ecophysiological (e.g., Ruffault et al. 2022) or eco-evolutionary models (e.g., Cotto et al. 2017).

4.4 Risk of maladaptation in maritime pine and limitations

No region was consistently identified as being most at risk of maladaptation across the maritime pine range in the different genomic offset predictions produced in our study, and virtually any region could be flagged as highly vulnerable depending on the specific combination of method, SNP set, and general circulation model used for the projections. In

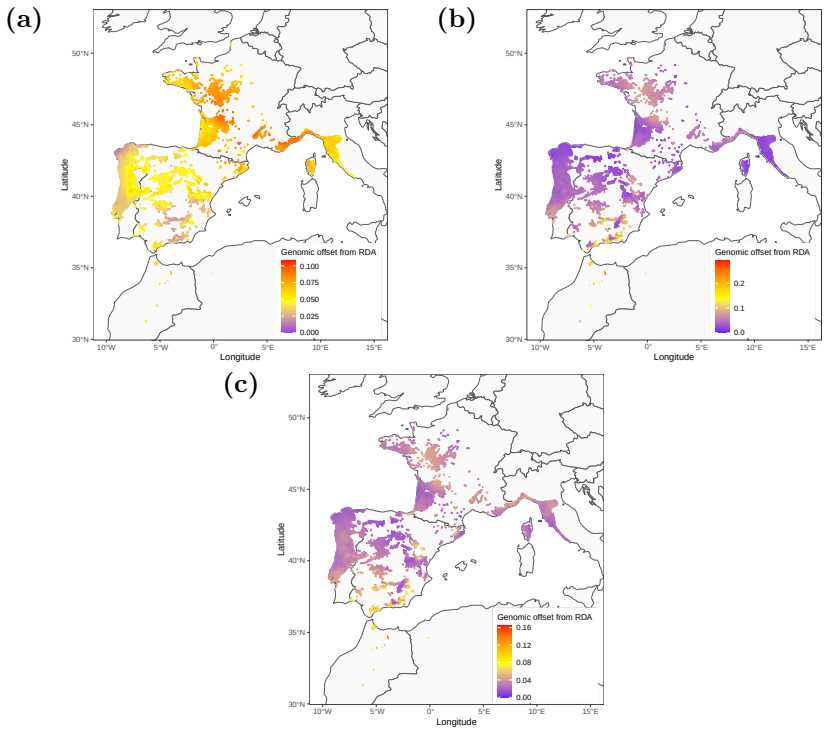

Figure 8: Projections of genomic offset predictions from RDA and (a) the set with all the candidate SNPs (380 SNPs), (b) the set with common candidate SNPs (69 SNPs) and (c) the set with the candidate SNPs corrected for population genentic structure (221 SNPs). These predictions correspond to the averaged genomic offset predictions across the five climate general circulation models, using the period 1901-1950 for the reference climates, and the period 2041-2060 for the future climates under the shared socio-economic pathway (SSP) 3.7-0 (see section 2.7 and table 1, first column).

this section, we focus on predictions from RDA models based on the three sets of candidate SNPs, as these models exhibited the highest validation accuracy in the inventory plots—whereas the common garden validations did not allow for clear discrimination among methods or SNP sets. Populations in central and southwestern France were identified as having higher risk of future maladaptation by RDA based on all candidate SNPs, whereas RDA predictions based on the other two sets of candidate SNPs primarily identified regions in southeastern Spain and northern Africa (fig. 8). At the population level, Oria (ORI; southeastern Spain), Tamrabta (TAM; North Africa), and Cómpeta (COM; southeastern Spain) exhibited the highest predicted genomic offset with RDA based on the common candidate SNPs and candidate SNPs corrected for population genetic structure, whereas these same populations showed among the lowest genomic offset values under RDA predictions using

all candidate SNPs. In contrast, RDA predictions based on all candidate SNPs identified Pineta (PIE; Corsica), Olonne-sur-Mer (OLO; French Atlantic), and Saint-Jean-des-Monts (STF; French Atlantic) as being most at risk of maladaptation. Given the high degree of inconsistency across genomic offset predictions—even among those with the best empirical validation—these results must be interpreted with considerable caution. We conclude that current genomic offset methods are not yet mature enough to provide consistent and reliable metrics for assessing maladaptation risk in maritime pine.

Data limitations inherent to our study may partly explain these inconsistent results. First, the population allele frequencies used to predict genomic offset were based on small sample sizes for certain populations, notably Madisouka (MAD), which had only one individual available (table S4). To maximize the number of populations, we included this genotype in our analyses, despite the trade-off in individual sample sizes. Nevertheless, the average number of samples per population is about 13 diploid individuals, which should still be sufficient for allele frequency estimation in most populations. Second, our study used 9,817 SNPs—a relatively small number given the large size of the maritime pine genome (28 Gbp; Zonneveld 2012). We filtered out SNPs with more than 20% missing data and imputed the missing values for the remaining SNPs using the most common allele at each SNP within the main gene pool of the individual. We verified that this imputation step did not introduce any bias by confirming a high correlation between genomic offset predictions based on all SNPs and those based on the subset of 3,258 SNPs with no missing data. Despite these data limitations, the genomic offset projections from GF observed in our study align with those reported in a recent study which used a larger dataset of 1,510 individuals from 82 maritime pine populations (about 50 populations with sample size over 20 diploid individuals; Ther-

aroz et al. 2024). Both studies identified the populations of Armayán (ARM), Alto de la Llama (ALT) and Sergude (SEG) as having some of the highest genomic offset values. This consistency between studies supports the adequacy of our data to conduct this study.

The inconsistency of our results may be better explained by the strong limitations inherent to the genomic offset approach, which have already been discussed in depth (Hoffmann et al. 2021, Rellstab et al. 2021, Lotterhos 2024a, Ahrens et al. 2025, Lind and Lotterhos 2025). We will mention here just a few arguments that we consider should be given particular attention in maritime pine, and more generally in forest trees. First, climate change exposure is integrated within the genomic offset approach using distances between long-term means of past and future climatic conditions. However, population vulnerability to climate change will also strongly depend on the variation and correlation of the climatic variables, and the magnitude and probability of climatic extremes (Parmesan et al. 2000, Nadeau and Fuller 2015). For example, in forest trees, die-offs have been attributed to increasingly frequent and intense drought events (Allen et al. 2010, 2015). In this line, Lind and Lotterhos (2025) demonstrated that the predictive ability of genomic offset strongly decreased under climate novelty, particularly in study systems with strong local adaptation. Second, vulnerability to climate change is not only determined by the risk of maladaptation but also by the ability of a population to respond to the changes. This intraspecific response capacity relies on three mechanisms: phenotypic plasticity, dispersal ability and adaptive potential (IPCC 2007, Foden et al. 2019). Most tree species show high phenotypic plasticity (Nicotra et al. 2010, Benito Garzón et al. 2019), long-distance gene flow facilitating the spread of beneficial alleles (Kremer et al. 2012), and high levels of genetic variation within populations (Scotti et al. 2016). Since these components of population response capacity are not integrated into

the genomic offset approach, any credible interpretation of its predictions must take this context into account.

A final caveat of our study is the use of contemporary genetic data to predict the effects of recent climate change; ideally, genetic samples would be collected from populations before the onset of climate shifts. Accumulating evidence suggests that tree populations can evolve rapidly (e.g., Petit and Hampe 2006, Saleh et al. 2022), and thus we cannot rule out that the genomic composition of the sampled populations has changed significantly over the last century.

5 Conclusion

Our study shows that current genomic offset approaches produce highly variable outcomes depending on technical choices. Grounding these approaches in a more solid theoretical framework appears necessary. Progress has already been made in defining a quantitative theory and the domain of applicability of genomic offset approaches (Hoffmann et al. 2021, Rellstab et al. 2021, Gain et al. 2023, Lotterhos 2024a, Ahrens et al. 2025). Empirical validation based on diverse data sources (e.g., natural populations vs common gardens, multi-environment common gardens, multiple traits, multiple species, etc) and evaluation approaches (e.g., local-foreign vs home-away fitness offsets; Lotterhos 2024a) will also be needed before the genomic offset concept can be confidently applied in conservation and management strategies as a metric of maladaptation.

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7 Author contributions

SCG-M designed the experiment and supervised the curation of field data. MdM cleaned and formatted the phenotypic data in the common gardens. MM extracted the climatic values at the location of the populations and the National Forest Inventory (NFI) plots, and provided the raster files to project the genomic offset predictions across the species range. F Bagnoli, SCG-M and GGV did the DNA extractions, production, cleaning and checking of the genomic data. AC cleaned and formatted mortality data from the NFI plots. SCG-M, JA and MBG conceived the paper methodology. JA and F Barraquand built the Bayesian models and codes in the validation steps. JA conducted the data analyses. JA led the writing of the manuscript. All authors interpreted the results, contributed to the writing of the manuscript and gave final approval for publication.

8 Data and code availability

Data and code were deposited in the Dryad repository at https://doi.org/10.5061/dryad.bnzs7h4jt. The scripts are also available in the following Github repository: https://github.com/JulietteArchambeau/GOPredEvalPinpin.

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