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RESEARCH ARTICLE

# Data reconciliation in multi-trait experiments with kinship ordination

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## Abstract

1. A central aim in biology is understanding the heritability of traits and how trait interactions contribute to success in diverse environments. Experiments that record multiple traits from individuals of known pedigree or genetic relatedness in distinct environments are key to addressing this aim. Mixed modelling approaches have been proposed for analysing such multivariate trait data. The parameter space of these mixed models grows quadratically with the number of traits and environments considered, which increases computational demand and the risk of overfitting. Existing approaches can also be challenging to implement for datasets in which different traits were measured in different environments.
2. We developed a latent variable model that incorporates genetic marker data for estimating heritability and improving predictions of traits. Our approach promotes model parsimony by estimating environmental associations and genetic variances for a reduced number of latent traits. The model can accommodate variation in genetic correlations across environments and can be applied in settings where only a subset of traits is observed in each environment, maximizing use of the data. We show that existing model-based ordination methods can be viewed as simplifications of our approach.
3. In a simulation study, we found that our approach improves sampling efficiency by an order of magnitude relative to standard multivariate mixed modelling approaches. Compared with existing ordination methods, our approach also improved inference for environmental associations and predictive performance. We applied our model to reconcile partially overlapping datasets collected from

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growth chamber and common garden experiments of *Bromus tectorum*, an annual grass invasive to the United States. Fitting mixed models independently to the data sources resulted in biologically unreasonable estimates of narrow-sense heritability, and a joint analysis with our latent variable model improved inference. Drawing from the joint analysis, we present a holistic explanation for the strength of several clines in *Bromus tectorum* and discuss their relevance for invasion in the Intermountain West.

4. The flexibility, tractability and performance of our approach make it appealing for joint inference and prediction in experiments of multiple traits. More broadly, we demonstrate the value of incorporating genetic marker data into latent variable models.

**KEYWORDS**
*Bromus tectorum*, common garden experiments, heritability, latent variable modelling, multivariate mixed modelling, reduced rank, trait selection

## 1 | INTRODUCTION

Predicting the demographic success of a species involves understanding which traits are favoured in unique environments as well as how heritability differs across environments (Lande, 1979). For decades, breeders have addressed this question with multi-trait multi-environment trials, where genetically identical plants are grown in several environments to perform genomic selection on multiple traits and improve crop yields (Endelman, 2023; Gill et al., 2021; Montesinos-López et al., 2016; Sandhu et al., 2022). Related common garden experiments have been adopted by ecologists to understand intraspecific trait variation in relation to climate and many other factors (de Villemereuil et al., 2016; Schwinning et al., 2022). Although these experiments provide a gold standard for learning about the effects of environment and genotype on phenotype, it is often infeasible to record each trait for every genotype in all environments. For example, certain traits may be time-consuming or expensive to record (Li et al., 2023) and, therefore, only observed for a subset of genotypes and environments. This leads to uneven sample sizes and differences in the number of observed traits across environments, which may not be amenable to existing statistical methods (Zipkin et al., 2021).

A joint analysis of multivariate trait data has many advantages. Models that accommodate multiple traits can outperform univariate models, particularly for incomplete datasets where some traits may not have been collected in each environment or were collected for a reduced number of genotypes (He et al., 2016; Lee & Van der Werf, 2016; Schulthess et al., 2018). In these contexts, multi-trait models provide a way to predict unmeasured traits using the information learned in the observed traits (Montesinos-López et al., 2016). Multi-trait models use the full dataset, which generally increases the precision of heritability estimates and other biologically relevant quantities (Montesinos-López et al., 2016; Zipkin et al., 2021). Combining information from multiple traits improves power to detect genotype–phenotype and environment–phenotype associations (Ahlinder et al., 2024; Van der Sluis et al., 2013). Multi-trait models better characterize joint evolutionary selection pressures than univariate models (Kruuk, 2004) and can reduce trait selection bias (Pollak et al., 1984).

Traditional approaches to analysing multi-trait data have followed a mixed modelling framework (Henderson, 1975), and various extensions have been proposed (Ahlinder et al., 2024; Ahlinder & Sillanpää, 2013; Bauer et al., 2009; Hallander et al., 2010; Mathew et al., 2012; Waldmann et al., 2008). Key improvements include accommodating missing data, constraining credible intervals to the natural support of each parameter, modelling non-linear genetic effects (e.g. dominance and epistasis), error propagation and reduced runtime. One persistent drawback of the mixed modelling approach is that the parameter space grows quadratically with the number of traits and environments considered (Ahlinder et al., 2024). The large number of parameters is challenging to accurately estimate using datasets with many traits but few genotypes (Johnstone & Titterington, 2009). Estimating the variance components jointly can also be computationally demanding and is prone to convergence issues (Ahlinder & Sillanpää, 2013; Misztal, 2008).

Several methods have been proposed to facilitate model parsimony and computation in the analysis of multivariate data. Tipping and Bishop (1999) introduced probabilistic principal component analysis and motivated it as a special case of factor analysis (Bartholomew et al., 2011). Geneticists quickly adopted probabilistic principal component analysis for missing data imputation (Oba et al., 2003). Tipton et al. (2017) used probabilistic principal component analysis to infer spatio-temporal trends in climate from sparse historical records. Likewise, various factor analysis models have been proposed for heritability estimation and genomic prediction in agronomy (Azevedo et al., 2023) and animal breeding (Meyer, 2007). While the previous modelling frameworks assume a Gaussian likelihood, a wider class of latent variable models

generalizes the previous approaches for non-normally distributed multivariate data. In particular, various generalized linear latent variable modelling frameworks have been proposed in the context of joint species distribution models (Hui et al., 2015; Ovaskainen et al., 2017; Popovic et al., 2022; van der Veen et al., 2021, 2023; Warton et al., 2015).

In this work, we demonstrate the scalability and flexibility of latent variable models for providing joint inference from experiments with varying trait collections. Our approach involves reconstructing the observed traits from a lower-dimensional collection of unobserved traits. The unobserved traits efficiently describe shared patterns in traits that are often described as life-history strategies. The unobserved traits correspond to the latent variables and are connected to the observed traits using a factor analysis framework. We include covariates and genomic dependence in the mean and covariance structure of the latent variables to accommodate variation in traits across environments and genotypes, respectively. Our approach provides inference for trait-specific environmental associations and genetic variances but allows us to estimate these quantities using the lower-dimensional representation of traits, thereby facilitating model parsimony and computation.

As in spatial latent variable modelling frameworks, the lower-dimensional representation of traits induces regularization (Stein, 2014). Regularization increases bias for the trait-specific environmental associations and genetic variances but decreases variance. The motivation for regularization is that reductions in variance will generally outweigh losses in accuracy because of increases in bias (Gelman & Rubin, 1992), but this may not always be true. In the context of joint species distribution models, Pichler and Hartig (2021) found that latent variable models resulted in lower accuracy for species–species associations relative to models fit using a full-rank species covariance matrix. Regularization is also frequently used for identifying associations in settings of sparsity (Bogdan et al., 2011; Carvalho et al., 2010; Tibshirani, 1996). We consider sparse multi-trait experiments where certain traits may not have been measured in all environments. Although most existing approaches to prediction and heritability estimation can handle missing observations (Ahlinder et al., 2024; Endelman, 2011; Hadfield, 2010; Isik et al., 2017; Pérez & de Los Campos, 2014), we are unaware of approaches that provide joint Bayesian inference for contexts in which the number of traits measured differs by environment. Latent variable models provide a principled approach for estimating heritability and environmental associations in this context.

We highlight the flexibility of our approach in a data reconciliation analysis (Hanks et al., 2011) of a multi-trait experiment for *Bromus tectorum* (cheatgrass). *Bromus tectorum* is an annual grass native to Eurasia and northern Africa. Today, *B. tectorum* is globally distributed as a result of several invasions. In the Intermountain West of the United States, the invasion of *B. tectorum* has degraded local ecosystems (Germino et al., 2016). *Bromus tectorum* produces highly flammable litter that increases wildfire occurrence, which can reinforce its selective advantage over native species and promote landscape dominance (Balch et al., 2013; Brooks et al., 2004). Invasion in the Intermountain West has also been bolstered by multiple introductions of *B. tectorum* (Mack, 1981) that have increased genetic diversity (Gamba et al., 2025). As a result, there is large phenotypic variation in traits such as flowering time that have contributed to the success of *B. tectorum* in a wide range of environments (Howell et al., 2020; Hufft & Zelikova, 2016; Vahsen et al., 2025). An analytical challenge to predicting the geographical spread and evolution of *B. tectorum* under climate change is identifying the traits and life-history strategies that contribute to *B. tectorum* success in different environments and estimating the heritability and genetic correlations of these traits. We used our approach to facilitate joint inference from physiological, growth chamber, and common garden experiments of *B. tectorum*.

## 2 | METHODS

### 2.1 | Review of the mixed modelling approach

Multi-trait data are generally analysed using a mixed modelling approach. Suppose that we measured a trait for a collection of individuals comprising $G$ genotypes. We could specify a mixed model as

$$y_{i,g} \sim [y_g \mid \mu_g, \boldsymbol{\phi}], \tag{1}$$

$$\mu_g \sim \mathcal{N}(\theta_g, \sigma^2), \tag{2}$$

where we use the bracket notation to represent probability distributions (Gelfand & Smith, 1990) in Equation (1), $y_{i,g}$ denotes the observed trait for replicate $i = 1, \ldots, n_g$ (i.e. individual plant) of genotype $g = 1, \ldots, G$, $\boldsymbol{\phi}$ is a vector of additional parameters besides the mean $\mu_g$ in the likelihood, $\theta_g$ is a genotype random effect, and we have assumed the traits have been centred to have mean zero. For brevity, we use the notation '~' to define conditional distributions instead of explicitly writing $\mu_g \mid \theta_g, \sigma^2 \sim \mathcal{N}(\theta_g, \sigma^2)$ as in Equation (2), for example. In multi-trait experiments (Endelman, 2023; Gill et al., 2021), individual level variation is often ignored (i.e. $\mu_g = \bar{y}_{i,g} = \sum_{i=1}^{n_g} \frac{y_{ig}}{n_g}$), but for completeness, we retain the more general setup. The random effects are specified as

$$\boldsymbol{\theta} \sim \mathcal{N}(\mathbf{0}, \zeta^2 \boldsymbol{K}), \tag{3}$$

where $\boldsymbol{\theta} = (\theta_1, \ldots, \theta_G)'$, $\boldsymbol{K}$ describes the pedigree or kinship of the $G$ genotypes, and $\zeta^2$ is the additive genetic variance. The variance, $\zeta^2$, does not include effects related to gene interactions (epistasis) and dominance (Hill et al., 2008), and is an underestimate of the total genetic contribution to phenotype. The matrix $\boldsymbol{K}$ enters the model as data and is either known from the pedigree of the $G$ genotypes or calculated from genetic marker data. Incorporating the proportional random effect structure within a mixed modelling approach has been referred to as the 'animal model' (Lynch et al., 1998) because of its popularity in the animal breeding literature.

The narrow-sense heritability (Wilson et al., 2010) of the trait is

$$h^2 = \frac{\zeta^2}{\zeta^2 + \sigma^2}. \tag{4}$$

Equation (4) describes the proportion of total phenotypic variation in the trait that can be explained by additive genetic variance. An implicit assumption is that many small-effect mutations contribute to trait variation. If a trait is influenced by a few large-effect loci, additive or not, heritability estimates will be unreliable because closely related individuals can still have vastly different phenotypes.

Extensions of the mixed model accommodate multiple traits and environments (Endelman, 2023; Gill et al., 2021; Montesinos-López et al., 2016; Sandhu et al., 2022). For example, suppose $\mu_{g,t,e}$ denotes the trait mean for genotype $g$ of trait $t = 1, \ldots, T$ in environment $e = 1, \ldots, E$. A multivariate mixed model for these trait means could be specified as

$$\mu_{g,t,e} \sim \mathcal{N}\left(\boldsymbol{x}_e'\boldsymbol{\beta}_t + \theta_{g,t,e}, \sigma^2_{t,e}\right), \tag{5}$$

where $\boldsymbol{x}_e$ is a $p$-dimensional vector of covariates measured in environment $e$, $\boldsymbol{\beta}_t$ are trait specific covariate associations, $\theta_{g,t,e}$ is the genomic random effect, and $\sigma^2_{t,e}$ accounts for residual variation. Furthermore, let $\boldsymbol{\Theta}$ denote an array with $G$ rows, $T$ columns, and $E$ slices containing the random effects. A generic model for the random effects is as follows

$$\text{vec}(\boldsymbol{\Theta}) \sim \mathcal{N}(\boldsymbol{0}, \boldsymbol{K} \otimes \boldsymbol{\Sigma}), \tag{6}$$

where $\text{vec}(\boldsymbol{\Theta})$ denotes the vectorization of $\boldsymbol{\Theta}$, $\otimes$ is the Kronecker product, and $\boldsymbol{\Sigma}$ is a square matrix with $T \times E$ columns, which may be diagonal, block-diagonal, dense, etc., depending on the application.

We specified $\boldsymbol{\Sigma}$ as block-diagonal matrix of the form $\boldsymbol{\Sigma} = \text{block-diag}\{\boldsymbol{\Sigma}_1, \ldots, \boldsymbol{\Sigma}_E\}$, such that the genomic random effects, $\theta_{g,t,e}$, were independent across environments. The covariance between traits in environment $e$ was modelled as

$$\boldsymbol{\Sigma}_e = \boldsymbol{Z}_e \boldsymbol{R} \boldsymbol{Z}_e, \tag{7}$$

where $\boldsymbol{R}$ is a correlation matrix and $\boldsymbol{Z}_e = \text{diag}\{\zeta_{1,e}, \ldots, \zeta_{T,e}\}$ is a diagonal matrix of standard deviations. The implied heritability of trait $t$ in environment $e$ from Equation (7) is given by $\frac{\zeta^2_{t,e}}{\zeta^2_{t,e} + \sigma^2_{t,e}}$.

Although the mixed model has been central to estimating heritability and genomic prediction for countless traits and wild populations, the approach has several limitations. Practical applications of the mixed model often need to account for multiple sources of variability that require additional random effects that can cause convergence and parameter identifiability issues (Ahlinder et al., 2024). Even for the relatively simple covariance structure specified in Equation (7), the number of parameters in the multivariate mixed model grows quadratically with the number of traits and trait-by-environment combinations. Extending the mixed model for joint analysis of multiple data types where the number of traits and genotypes vary by environment is also challenging. In the following section, we describe a latent variable modelling approach that addresses the aforementioned limitations.

## 2.2 | The latent variable modelling approach

We developed a latent variable model for the multivariate analysis of correlated traits. As before, $\mu_{g,t,e}$ denotes the mean of genotype $g$ for trait $t$ in environment $e$. We proposed modelling the trait means using the linear model

$$\boldsymbol{\mu}_{g,\cdot,e} \sim \mathcal{N}\left(\boldsymbol{W}\boldsymbol{\alpha}_{g,\cdot,e}, \text{diag}\left\{\sigma^2_{1,e}, \ldots, \sigma^2_{T,e}\right\}\right), \tag{8}$$

where we use the notation '$\cdot$' to denote all elements along a dimension, $\boldsymbol{W}$ is a factor matrix of dimension $T \times q$, and $q$ is the number of latent variables. We modelled the joint distribution of genotype values, $\boldsymbol{\alpha}_{\cdot,l,e} = (\alpha_{1,l,e}, \ldots, \alpha_{G,l,e})'$, for latent variable $l = 1, \ldots, q$ as

$$\boldsymbol{\alpha}_{\cdot,l,e} \sim \mathcal{N}\left(\{\boldsymbol{x}_e'\boldsymbol{\eta}_l\}\boldsymbol{1}, \zeta^2_{l,e}\boldsymbol{K}\right), \tag{9}$$

where $\boldsymbol{1}$ is a $G$-length vector of ones and $\boldsymbol{K}$ is the kinship matrix, as before. In the joint distribution, Equation (9), we accommodated collective differences in all genotypes across environments in the mean structure and variation across genotypes in the covariance matrix. Our model restricts the covariance among the latent variables to be proportional to kinship, but modelling frameworks that relax this assumption have been proposed (van der Veen & O'Hara, 2024).

The connection between our approach and the multivariate mixed model can be seen by marginalizing over the latent variables. The resulting joint distribution for the vector of genotype means of trait $t$ in environment $e$ was

$$\boldsymbol{\mu}_{\cdot,t,e} \sim \mathcal{N}\left(\boldsymbol{x}_e'\left\{\sum_{l=1}^{q} w_{t,l}\boldsymbol{\eta}_l\right\}\boldsymbol{1}, \sigma^2_{t,e}\boldsymbol{I} + \left\{\sum_{l=1}^{q} \zeta^2_{l,e} w^2_{t,l}\right\}\boldsymbol{K}\right), \tag{10}$$

where $w_{t,l}$ denotes the value from the $t$th row and $l$th column of $\boldsymbol{W}$ and $\boldsymbol{I}$ denotes a $G \times G$ identity matrix. From Equation (10), the implied association between trait $t$ and environmental covariates, $\boldsymbol{x}_e$, is

$$\boldsymbol{\beta}_t = \sum_{l=1}^{q} w_{t,l}\boldsymbol{\eta}_l. \tag{11}$$

The regression coefficients, $\boldsymbol{\beta}_t$, in (11) are analogous to those in Equation (5), but the latent variable models provides a more parsimonious estimator of the quantity (van der Veen et al., 2021, 2023) similar to reduced rank regression (Davies & Tso, 1982). Similarly, the implied additive genetic variation in $\boldsymbol{\mu}_{\cdot,t,e}$ is $\sum_{l=1}^{q} \zeta^2_{l,e} w^2_{t,l}$. We can estimate the genetic covariance between traits $t$ and $t^\star$ in environment $e$ (i.e. the off-diagonal elements of the trait genetic covariance matrix: Lande, 1979) with $\sum_{l=1}^{q} \zeta^2_{l,e} w_{t,l} w_{t^\star,l}$. We quantified the narrow-sense heritability of trait $t$ in environment $e$ as the derived quantity

$$h^2_{t,e} = \frac{\sum_{l=1}^{q_e} \zeta^2_{l,e} w^2_{t,l}}{\sum_{l=1}^{q_e} \zeta^2_{l,e} w^2_{t,l} + \sigma^2_{t,e}}. \tag{12}$$

Our estimates of $h^2_{t,e}$ are conditional on $\boldsymbol{\beta}_t$ in that we are estimating heritability in environment $e$ controlling for environmental variation that we

can describe based on the covariates, $\boldsymbol{x}_e$. All other sources of variation including dominance and epistatic genetic effects, phenotypic plasticity, and environmental factors that were not included in $\boldsymbol{x}_e$ are captured in the variance term, $\sigma^2_{t,e}$, which we refer to as the error variance, and is distinct from individual level variation (i.e. $\text{Var}(y_{i,g,t,e})$).

The latent variable model, as described in Equation (10), is overparameterized and requires additional constraints for the quantities to be individually identifiable (Huber et al., 2004). In particular, the factor matrix, $\boldsymbol{W}$, suffers from sign, permutation and rotation invariance (Papastamoulis & Ntzoufras, 2022). As a result, the coefficients $\boldsymbol{\eta}_l$ and $\zeta^2_{l,e}$ are also not identifiable. Geweke and Zhou (1996) proposed a lower triangular constraint on $\boldsymbol{W}$ that addresses the aforementioned issues, but this approach induces order dependence in the traits (Bhattacharya & Dunson, 2011) and complicates prior specification for $h^2_{t,e}$ in our modelling framework. We adopted the approach proposed by Papastamoulis and Ntzoufras (2022), which involves fitting the overspecified model and correcting the invariance of the MCMC sample using a post-processing scheme. Post-processing is only required to standardize inference for $\boldsymbol{W}$, $\boldsymbol{\eta}_l$, and $\zeta^2_{l,e}$. No post-processing is required for the lower rank estimators of regression coefficients (11) and heritability (12). A full description of these issues and their resolution is provided in the Supporting Information, along with additional details regarding prior distributions. In short, our prior specifications were motivated by inducing an approximately uniform prior distribution on heritability regardless of the number of selected latent variables. We also implemented a hierarchical prior for the error variances to account for repeated measurements of the same trait across environments.

Our proposed latent variable modelling approach estimates genetic variances and environmental associations for $q$ unobserved traits and uses the factor matrix to infer the implied environmental associations and genetic variances for the observed traits. The advantage of this approach is that, if traits are correlated, we can choose $q < T$ to achieve a lower-dimensional representation of traits and more parsimonious model. For example, instead of estimating environmental associations for all $T$ traits, we need only estimate the associations for $q$ latent traits, simplifying posterior computation. With regard to parameter estimation and posterior predictions, choosing $q < T$ latent variables may increase posterior mean bias but decreases posterior variances. Generally in parsimonious models, the reductions in variance outweigh losses in performance because of increases in bias (Gelman & Rubin, 1992).

The multivariate mixed model, Equation (5), has $G \times T \times E$ latent parameters because of the random effects, $\theta_{g,t,e}$ in Equation (6), specified for the mean of each trait. In contrast, our proposed model has $G \times q \times E$ latent parameters, which can be a substantial reduction for $q << T$. Likewise, given the block-diagonal structure specified in Equation (7), the multivariate mixed model has $(T^2 - T)/2$ free parameters in the correlation matrix $\boldsymbol{R}$ and $T \times E$ genetic variances, $\zeta^2_{t,e}$. In our latent variable model, correlation in trait means is modelled as a function of $\boldsymbol{W}$, which is of dimension $T \times q$, and genetic variances are a function of $q \times E$ latent variance terms (i.e. $\zeta^2_{l,e}$). Furthermore, note that given the typical identifiability constraints, there are effectively $Tq - (q^2 + q)/2$ free parameters in $\boldsymbol{W}$ (Robinson, 1973). In either case, for fixed $q$, the number of parameters in our models grows linearly with $T$ and $E$ whereas, in the multivariate mixed model, the number grows quadratically in $T$ and $T \times E$.

Similar reduced rank approaches for multivariate data have been proposed in the context of joint species distribution modelling (Warton et al., 2015). Pollock et al. (2014) proposed the following generalized linear mixed model for understanding co-occurrence patterns in species:

$$y_{j,e} \sim \left[y_{j,e} \middle| \mu_{j,e}, \boldsymbol{\phi}\right], \tag{13}$$

$$\mu_{j,e} \sim \mathcal{N}\left(\boldsymbol{x}'_e \boldsymbol{\beta}_j, \boldsymbol{\Sigma}\right), \tag{14}$$

where $j = 1, \ldots, J$ and $e = 1, \ldots, E$ index species and environments, respectively, $\boldsymbol{\beta}_j$ are species specific regression coefficients, and $\boldsymbol{\Sigma}$ is a dense $J \times J$ species covariance matrix. Like the multivariate mixed model for multi-trait data, the parameters of the proposed joint species distribution model grows quadratically in the number of species considered. To facilitate parsimony, Warton et al. (2015) proposed modelling species correlations using model-based unconstrained ordination (Hui et al., 2015),

$$\mu_{j,e} = \boldsymbol{x}'_e \boldsymbol{\beta}_j + \boldsymbol{w}'_{j,\cdot} \boldsymbol{\alpha}_{\cdot,e}, \tag{15}$$

where $\boldsymbol{\alpha}_{\cdot,e} = (\alpha_{1,e}, \ldots, \alpha_{q,e})'$ is a $q$-dimensional vector of standard normal random variables, $\boldsymbol{w}_{j,\cdot} = (w_{j,1}, \ldots, w_{j,q})'$ is the $j$ row of the factor matrix, and their combination, $\boldsymbol{w}'_{j,\cdot} \boldsymbol{\alpha}_{\cdot,e}$, effectively replaces $\boldsymbol{\Sigma}$ in (14). A related approach, known as constrained ordination (Yee, 2004), reduces the dimension of the regression coefficients

$$\mu_{j,e} = \sum_{l=1}^{q} w_{j,l} \boldsymbol{x}'_e \boldsymbol{\beta}_l. \tag{16}$$

Concurrent ordination, as proposed by van der Veen et al. (2023), combines the previous two models,

$$\mu_{j,e} = \sum_{l=1}^{q} w_{j,l} \left(\boldsymbol{x}'_e \boldsymbol{\beta}_l + \alpha_{l,e}\right). \tag{17}$$

If we suppress knowledge of genotype, our proposed latent variable model is similar to concurrent and hierarchical ordination (O'Hara & Van Der Veen, 2024) where we treat traits as species. Given the connections of our proposed model to existing ordination methods, we refer to our approach as 'kinship ordination'.

Figure 1 provides an illustration of our approach in the context of a common garden experiment. Multiple traits of genetically identical plants are collected across several environments. We use our latent variable model to decompose the multivariate trait data into latent traits, which could represent life-history strategies. For example, the first latent trait/variable might capture a continuum of slow to fast life-history strategies. Genotypes collected from hotter environments may grow more rapidly, flower earlier in the year, and generally have fewer tillers, whereas 'cooler' genotypes have a slower growth rate, delayed flowering, and produce more tillers. Position along the

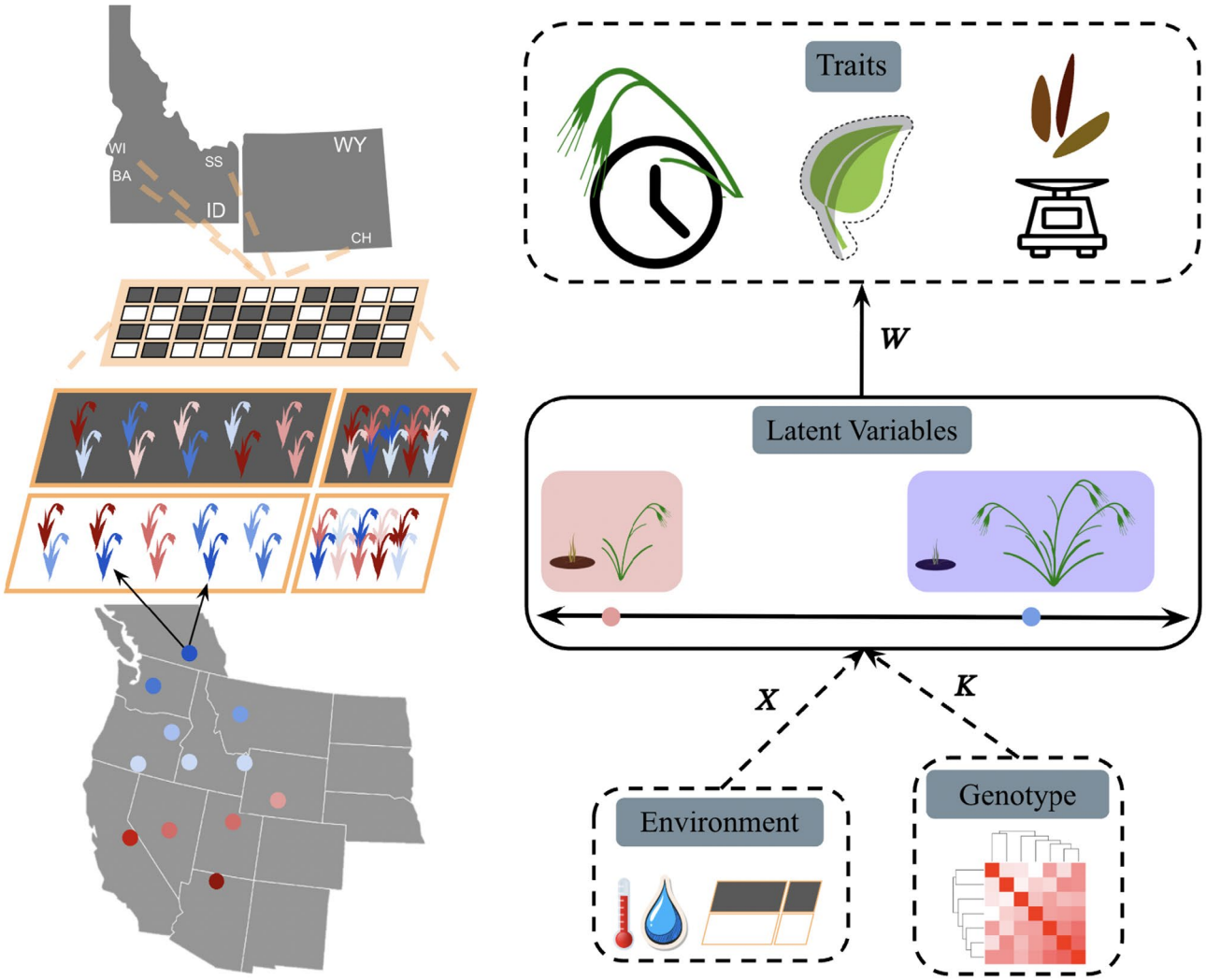



FIGURE 1 Illustration of kinship ordination model in context of *B. tectorum* multi-trait experiment. Left panel depicts common garden experiment and is adapted from Vahsen et al. (2025). Seeds from genotypes collected throughout the western United States were planted within plots of varying treatments (low versus high density crossed with low vs. high temperature, implemented with white and black gravel, respectively) at four sites in Idaho and Wyoming: Sheep Station, ID (44.2456, −112.2144); Baltzor, ID (43.2085, −116.9952); Wildcat, ID (43.4744, −116.9018); and Cheyenne, WY (41.2121, −104.8525). Traits including flowering time, specific leaf area, and seed mass were recorded for multiple genotypes. Traits were connected to lower-dimensional latent traits/variables through a factor matrix $\boldsymbol{W}$. Variation in latent variables across genotypes and environments was modelled as a function of current environment, $\boldsymbol{X}$, and kinship, $\boldsymbol{K}$. We use dashed and solid lines to denote observed and inferred quantities, respectively.

continuum is modelled as a function of current environment and genotype.

## 2.3 | Implementation

Software is available for fitting generalized linear latent variable models (Brooks et al., 2026; Clark & Wells, 2023; Korhonen et al., 2025; McGillycuddy et al., 2025; Niku et al., 2019, 2025; Tikhonov et al., 2020). None of this software can accommodate proportional covariance structures (i.e. the kinship matrix) in the distribution of the latent variables. Proportional covariance structures can be specified for phylogenetic random effects using `R` packages `Hmsc` and `gllvm`, but this is different from our specification in Equation (9). There is also software available for efficiently fitting multivariate mixed models with proportional covariance structures (Covarrubias-Pazaran, 2018).

We implemented the multivariate mixed model (MMM) and unconstrained (UO), constrained (CO), concurrent (CCO) and kinship ordination (KO) models using the probabilistic programming language `Stan` (Carpenter et al., 2017) within the statistical computing environment `R` (R Core Team, 2024). To improve sampling efficiency in the unconstrained, concurrent, and kinship ordination models (Stan Development Team, 2024), we marginalized over the latent variables in Equations (9), (15) and (17), respectively. In the Supporting Information, we describe how to draw samples of the latent variables from their full-conditional distributions in parallel using the posterior

sample of other parameters obtained with Hamiltonian Monte Carlo (HMC). While a subset of the described models can be fit more efficiently with the previously mentioned software, using a single probabilistic programming platform facilitates computational comparison by removing confounding factors such as the language or algorithms used to implement each model (Wilkinson et al., 2019). This also ensures a Bayesian implementation of each model, which simplifies assessing predictive performance and parameter estimation across models. As much as possible, we have also tried to use similar prior specifications such that differences in performance were a function of model structure alone. In both the simulation study and data reconciliation analysis, Sections 3 and 4 respectively, we ran the HMC algorithms for 1200 iterations with the first 200 iterations discarded as burn-in. The potential scale reduction factor (Gelman & Rubin, 1992) was less than 1.1 for all inferential quantities of interest indicating convergence. One subjective aspect of implementing latent variable models is choosing the number of latent variables. This decision may vary with objective (Tredennick et al., 2021). For example, with regard to data exploration, $q = 2$ latent variables is convenient for visualization. In our case, we sought to approximate the multivariate mixed model while reducing computational burden. This equates to picking a $q$ that meaningfully reduces the parameter space while still explaining a large proportion of the total trait variation. We used scree plots (Cattell, 1966) based on a standard principal components analysis of the raw trait data to select $q$. This approach is not directly applicable to experiments where the traits recorded in each environment varies because the full trait covariance matrix cannot be calculated. We used a combination of environment specific scree plots and prior knowledge to select $q$ in the *B. tectorum* analysis (Section 4).

## 3 | SIMULATION STUDY

We performed a simulation study to validate our KO approach and compare it with standard multivariate mixed and latent variable modelling approaches. The motivation of our study was to quantify differences in performance between approaches when the MMM is assumed to be the 'true' model. In particular, we sought to understand the potential drawbacks of applying our KO and other ordination approaches in contexts where fitting the MMM is not feasible either because of overparameterization or computational burden. In practice, the true model is not known, and latent variable models have been shown to outperform MMM for various real datasets (Azevedo et al., 2023).

We quantified differences in sampling efficiency (Efficiency) (Geyer, 1992), the calibrated Bayesian coverage (Coverage) proportion (Little, 2006), the bias (Bias) of posterior means, and the posterior standard deviations (Variability). Sampling efficiency captures differences in computational burden because of both run time and mixing, which can vary because of model structure. Bias and variability quantify parameter accuracy and precision, respectively. The coverage proportion is useful for understanding decreases in uncertainty that are helpful (i.e. posterior distributions more concentrated around the truth) versus those that are problematic (i.e. over-confident predictions or overly narrow credible intervals).

The aforementioned performance metrics pertain to parameter estimation and predictive performance, but note that the ordination methods described in Section 2.2 are primarily applied in ecology for data exploration and visualization (Hui et al., 2015). Nonetheless, existing ordination approaches provide a helpful baseline for quantifying the advantages of including genomic structure within the latent variables. Furthermore, even parameter estimation and prediction can be thought of as competing objectives (Tredennick et al., 2021). In the context of evolutionary biology and animal breeding, heritability estimation and genomic prediction coincide (Ahlinder & Sillanpää, 2013; Hill et al., 2008; Sillanpää, 2011). The simulation study quantified the ability of our KO approach to achieve similar parameter estimates and predictive performance to the MMM with fewer parameters, but note that overparameterization, when paired with regularization, can improve prediction (Hooten & Hobbs, 2015).

We simulated datasets from the MMM described in Equation (5) and, for simplicity, assumed a normal model (i.e., $y_{g,t,e} = \mu_{g,t,e}$). To induce strong correlations between traits, we set the off-diagonal elements of $\boldsymbol{R}$ to 0.9. Across simulations, we varied the total number of genotypes, traits, and environments. The vector $\boldsymbol{x}_i$ included an intercept and one continuous covariate. Parameter values were simulated using

$$\boldsymbol{\beta}_t \sim \mathcal{N}(\boldsymbol{0}, \boldsymbol{I}), \tag{18}$$

$$\sigma^2_{t,e} \sim \text{Gamma}(1, 1), \tag{19}$$

$$\zeta^2_{t,e} \sim \text{Gamma}(1, 1), \tag{20}$$

to induce a Uniform(0, 1) distribution on heritability. Biologically realistic kinship matrices, $\boldsymbol{K}$, were generated for each dataset by subsampling a random $G$ genotypes from a broader sample of 284 experimental mouse crosses provided in the `qtl2` package (Broman et al., 2019).

We fit all five models to 150 simulated datasets. For the ordination methods, we modelled $q$ latent variables, where $q$ was the number of components needed to explain at least 90% of the total trait variation based on a principal components analysis of the simulated trait data. This was between 3–5 and 6–8 principal components for datasets simulated with $T = 5$ and $T = 10$ traits, respectively. Prior specifications for $\boldsymbol{\beta}_t$, $\sigma^2_{t,e}$ and $\zeta^2_{t,e}$ were the same for all models and are provided in the Supporting Information. For the trait correlation matrix $\boldsymbol{R}$ in the MMM, we specified a LKJ prior (Lewandowski et al., 2009) with a shape parameter of 2.

Figure 2 summarizes the performance of the MMM and KO approaches with regard to heritability estimation for a variety of simulated datasets. Our KO approach increased sampling efficiency by up to an order of magnitude relative to the MMM. Gains in sampling efficiency scaled more slowly with the number of environments than for genotypes and traits. The MMM obtained the targeted nominal coverage rate of 90% for datasets simulated with relatively more genotypes and environments (i.e. $G = 50$ and $E = 10$), and

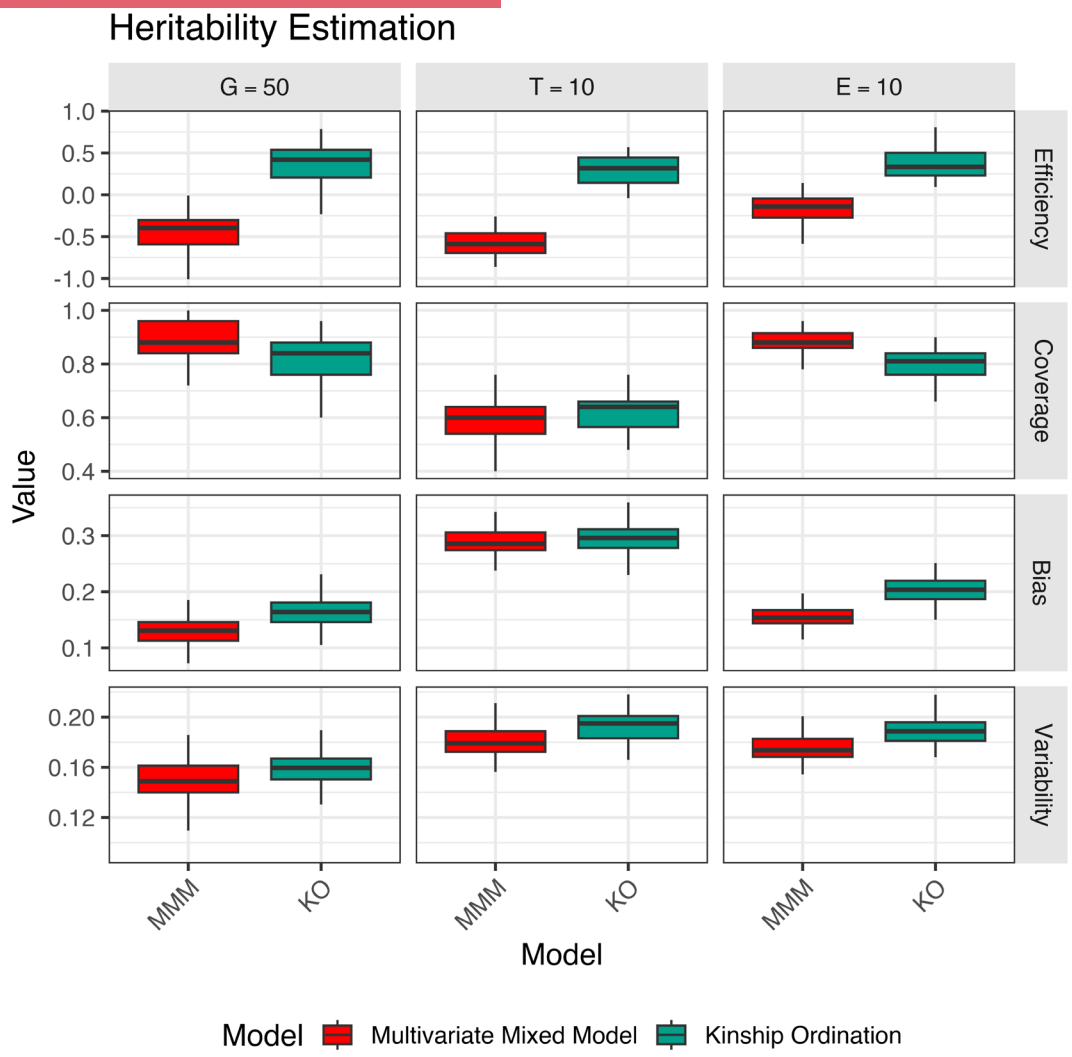



**FIGURE 2** Metrics for heritability estimation using multivariate mixed modelling and kinship ordination approaches. Row strip labels indicate the metric assessed, and column strip labels indicate the dimensions of the simulated datasets. Unless indicated otherwise (i.e., $G = 50$), data were simulated for $G = 25$ genotypes, $T = 5$ traits, and $E = 5$ environments. Efficiency is the logarithm, base 10, of the effective sampling rate (Geyer, 1992) in seconds. Coverage is the proportion of credible intervals that included the true simulated heritability. Bias is the absolute difference between the true heritability and posterior mean. Variability is the posterior standard deviation.

coverage was slightly lower for the KO approach. The KO approach also resulted in slightly higher bias and variability. For datasets with a greater number of traits (i.e. $T = 10$), both approaches resulted in lower coverage and greater bias and differences between approaches were less stark.

Figure 3 summarizes the performance of the MMM and selected ordination approaches for estimation of covariate associations, $\boldsymbol{\beta}_t$ in Equation (11). The ordination approaches increased sampling efficiency for $\boldsymbol{\beta}_t$ by at least an order of magnitude relative to the MMM approach, and constrained ordination was nearly 100 times more efficient. All models resulted in similar levels of bias. The ordination methods that did not account for kinship (i.e. concurrent and constrained) resulted in overly narrow credible intervals and poor coverage. Note that these approaches treat genotypes independently, which resulted in overly confident inference on $\boldsymbol{\beta}_t$. Our KO approach resulted in similar variability and coverage for datasets with a greater number of traits and environments, but slightly lower coverage than the MMM for datasets with more genotypes.

To quantify differences in out-of-sample predictive performance, we withheld 10% of randomly selected genotype–environment pairs from model fitting in each of the 150 simulated datasets. The ordination methods also improved sampling efficiency for posterior predictive distributions (Figure 4). Sampling efficiency was an order of magnitude faster for the kinship and concurrent ordination approaches relative to the MMM and even greater for constrained and unconstrained ordination. Models resulted in similar coverage for each dataset. In terms of predictive accuracy, the unconstrained ordination model provides a benchmark (i.e. the 'null' model) for quantifying the relative gains in performance related to accounting for environmental associations and kinship. Including covariates, as in the concurrent and constrained ordination models, decreased bias and variability by approximately 20%, whereas around a 40%

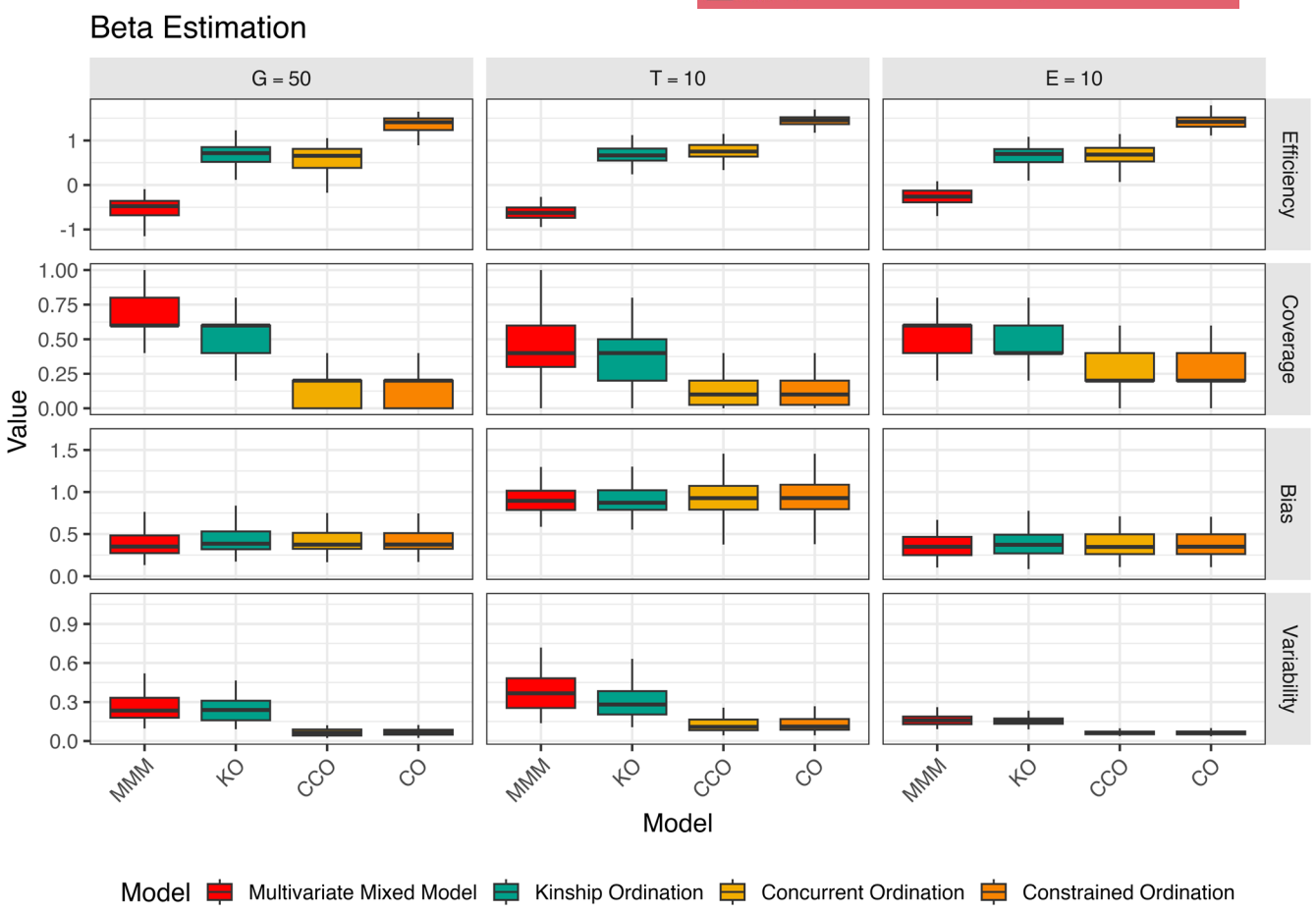



**FIGURE 3** Metrics for estimation of trait specific covariate associations, $\beta_t$, using multivariate mixed modelling and ordination approaches. Row strip labels indicate the metric assessed, and column strip labels indicate the dimensions of the simulated datasets. Unless stated otherwise (i.e. $G = 50$), data were simulated for $G = 25$ genotypes, $T = 5$ traits, and $E = 5$ environments. Efficiency is the logarithm, base 10, of the effective sampling rate (Geyer, 1992) in seconds. Coverage is the proportion of credible intervals that included the true simulated effect. Bias is the absolute difference between the true effect and posterior mean. Variability is the posterior standard deviation.

reduction was achieved by leveraging covariates and kinship as in the MMM and KO models. Overall, greater model complexity in the MMM was not associated with superior predictive performance relative to our KO approach.

## 4 | *BROMUS TECTORUM* DATA RECONCILIATION ANALYSIS

We collected seeds from over 200 *B. tectorum* individuals located in North America and Europe. Bulked seeds (i.e. grown for a generation in a common environment to reduce maternal effects on traits) from a subset of less than 100 individuals collected in the western United States were planted in four common gardens in Idaho and Wyoming (see Vahsen et al., 2025, for details). Permission for field studies was granted by the Idaho Department of Lands and the United States Department of Agriculture Agricultural Research Service. We planted seeds from each genotype in two densities under two different temperature treatments in a factorial design. Soil surface temperature was manipulated using black (high temperature) and white (low temperature) gravel and differed by 21°C on average between treatments (Maxwell et al., 2023). An illustration of the common garden experiment is provided in the left panel of Figure 1. At two sites, less than 20 genotypes were further analysed for physiological and morphological traits related to freezing tolerance and specific leaf area. We also planted seeds from the full collection of 200+ genotypes in a growth chamber environment. A total of 14 traits were recorded across all three experiments. The resulting dataset was sparse. Some traits were recorded in 17 environments and for nearly 100 genotypes while other traits were only recorded in two environments and for less than 20 genotypes. A full description of the experiments and traits collected is provided in the Supporting Information.

Following previous analyses of multi-trait experiments (Endelman, 2023; Gill et al., 2021), we summarized individual-level trait data by calculating the mean trait value across replicates, $\mu_{g,t,e} = \overline{y}_{i,g,t,e}$, treating the (possibly transformed) trait means as normally distributed. While estimates from linear mixed models have been shown to be robust to moderate deviations from normality (Schielzeth et al., 2020), these results do not directly translate to trait means calculated from count or binary data, particularly when

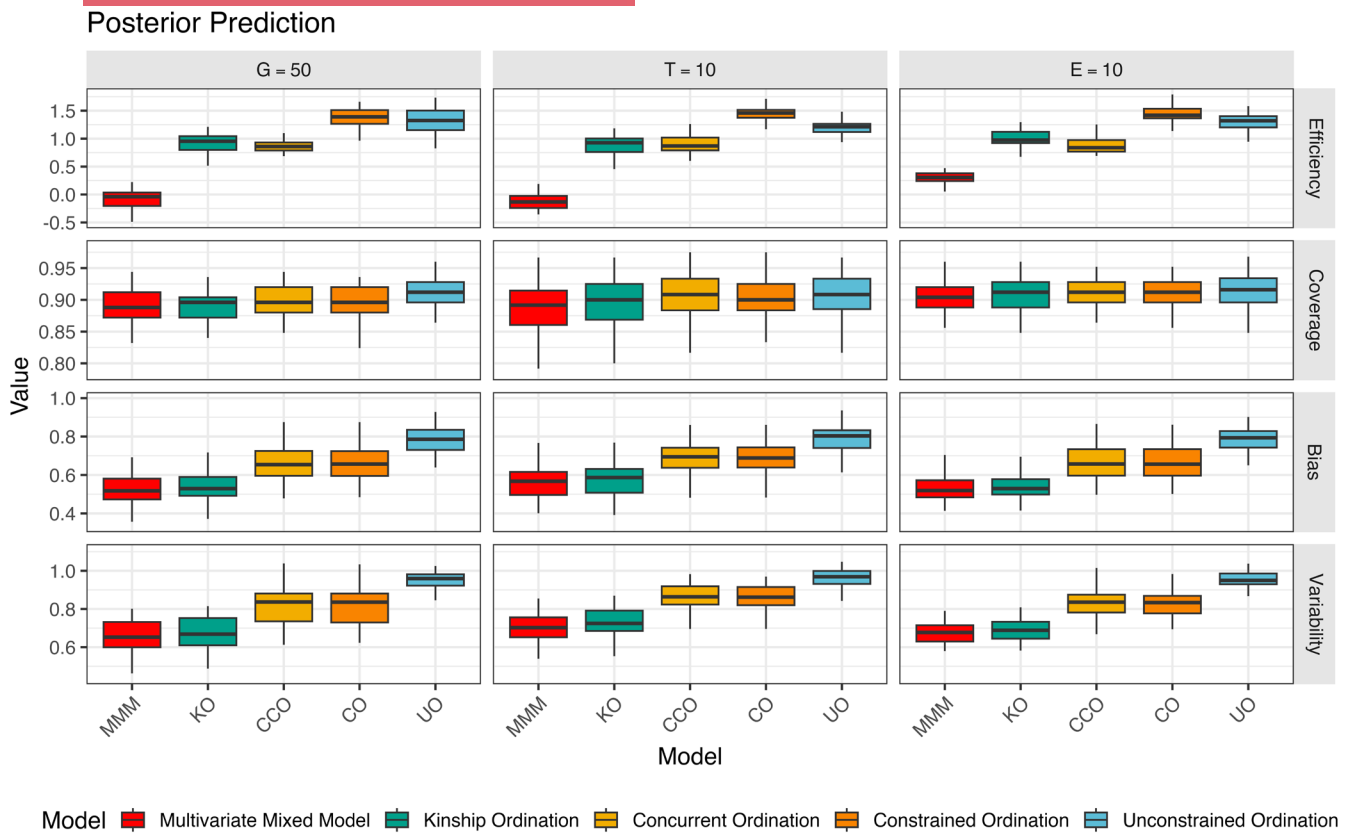



**FIGURE 4** Metrics for out-of-sample prediction of traits using multivariate mixed modelling and ordination approaches. Row strip labels indicate the metric assessed, and column strip labels indicate the dimensions of the simulated datasets. Unless stated otherwise (i.e. $G = 50$), data were simulated for $G = 25$ genotypes, $T = 5$ traits, and $E = 5$ environments. Efficiency is the logarithm, base 10, of the effective sampling rate (Geyer, 1992) in seconds. Coverage is the proportion of credible intervals that included the true trait value. Bias is the absolute difference between the true trait value and posterior mean. Variability is the posterior standard deviation of the posterior predictive distribution.

the number of replicates is small or when variance depends on the mean. Ives (2015) showed that linear models applied to transformed count data can, in some settings, exhibit lower type I error rates for environmental associations than Poisson and negative-binomial generalized linear models, but this advantage should be carefully weighed against several well-documented drawbacks (O'Hara & Kotze, 2010; Warton et al., 2016). In particular, we caution against normal models for highly variable traits or for trait means near the boundary of their natural support (e.g. survival probabilities near 0 or 1), where normal approximations may introduce substantial bias. In contexts where this is a concern, generalized linear latent variable models (Niku et al., 2019; Warton et al., 2015) or copula models (Popovic et al., 2022), if marginal distributions differ by trait, provide principled alternatives. For our analysis, all trait means were at least two standard errors away from their natural boundary, supporting the use of a normal approximation.

We fit the same models used in the simulation study, Section 3, to the *B. tectorum* trait means. The MMM, as specified in Equation (5), suffered from overparameterization for the *B. tectorum* multi-trait dataset. In particular, not all genetic variance parameters, $\zeta^2_{t,e}$, are identifiable because not all traits were measured in each environment. We obtained posterior inference by fitting independent MMMs to the subset of traits recorded in each experiment.

The covariates, $\boldsymbol{x}_e$, included unique intercepts for the growth chamber and four common garden treatments as well as two continuous covariates derived from a principal component analysis of 19 bioclimatic variables measured at the four common garden sites and seed source locations in the Intermountain West (Vahsen et al., 2025). The bioclimatic variables were derived from CHELSA 30-year (1981–2010) climate average data at ≈1 km resolution (Karger et al., 2017). The first principal component explained 37% of the total variation and depicts a continuum from cool and wet climates to hot and dry climates in seed source and experimental climates. The second principal component explained 24% of the total variation and depicts a continuum in environments from low to high temperature seasonality. An identity-by-state (IBS) kinship matrix, $\boldsymbol{K}$, was estimated for 215 genotypes using a dataset of 15, 101, 725 SNPs and the function `snpgdsIBS` in the `R` package `SNPRelate` (Zheng et al., 2012).

We choose $q = 4$ latent variables based on a combination of exploratory data analyses and prior knowledge. For the majority of environments, 90% of the total variation could be explained by four components based on a traditional principal component analysis applied to the raw trait data. Previous studies have suggested that

flowering time and seed mass are linked in *B. tectorum* with genotypes from desert environments having earlier phenology and producing larger seeds (Leger et al., 2009; Rice et al., 1992). Biomass and the number of seeds produced are similar measures of reproductive success. This leaves two free latent variables for explaining variation in the number of tillers and survival to reproduction, both of which are likely already partially represented in the first two latent variables. We assumed that variation in the remaining eight traits collected in a subset of environments could be accurately depicted with these same $q = 4$ latent variables.

Inference for heritability differed between approaches because of model structure and data utilization. The most direct comparison between methods is provided by comparing results for the growth chamber because the data from the common garden and physiology experiments only contributed to posterior inference through the hierarchical error variances associated with traits recorded in both experiments and the loading matrix $\boldsymbol{W}$. Hence, in the growth chamber, differences in inference were primarily a function of model structure. Point estimates of the MMM and posterior means of our KO approach were very similar for growth chamber traits with a Pearson correlation of $r = 0.89$ (Figure 5). The MMM resulted in a greater heritability and less uncertainty for total biomass (Biomass), survival to reproduction (Survival), total plant height (Height) and spring growth (Growth) than our KO approach. Credible intervals overlapped for all traits except Height and Growth.

For the six traits collected in each common garden environment (i.e. FT, Seed(n), Seed(m), Biomass, Tiller(n) and Survival), the posterior means of the MMM and our KO approach were moderately correlated ($r = 0.69$ on average across environments), but there were considerable differences in their 90% credible intervals. The credible intervals of the MMM were generally more narrow than the intervals of our KO approach, particular for production related traits (i.e. Seed(n), Biomass, Tiller(n)). The models provided similar mean estimates of heritability for flowering time (FT), per capita seed mass (Seed(m)) and survival to reproduction (Survival). With the exception of all treatments at Baltzor and the low density, low temperature (white gravel) treatment at Cheyenne, the heritability estimates of the MMM were near 1 for production-related traits and generally had little uncertainty. The heritability estimates of our KO approach were generally lower and had greater uncertainty. The posterior mean estimates of heritability inferred with our KO approach were also more variable across environments. Both methods suggested high narrow-sense heritability of flowering time (FT) in most environments, which has been observed in other species (Andrés & Coupland, 2012).

Discrepancies in the datasets used to fit each model were greatest for traits recorded in the physiology study (Phenological, Freeze, Fv/Fm, SLA). The MMM was fit to fewer than 20 genotypes for these four specific traits, whereas our KO approach used data from all three experiments. In addition, we could not include the same environmental covariates in the MMM because the physiology study traits were only recorded in two environments. The MMM resulted in dispersed posterior distributions that were similar to the prior distributions specified for heritability. Posterior distributions for heritability inferred with our KO approach were also dispersed but had less uncertainty than the MMM approach. In addition, their posterior means were greater at Wildcat than at Baltzor, which matched collective trends in heritability for the other six traits.

For some analyses, it may be more appropriate to classify traits related to reproductive success as outcomes. For example, in evolutionary biology, fitness outcomes are regressed against the remaining traits to understand selective pressures (Lande & Arnold, 1983). Selection coefficient estimates that exclude zero from these multiple regressions provide evidence that a trait is under selection. We used this approach to understand trait selection in invasive populations of *B. tectorum* in the Intermountain West. We calculated the logarithmic fitness of the 93 genotypes used in the common garden experiment as the natural logarithm of probability of reproduction plus the natural logarithm of the number of seeds produced. For each MCMC iteration, we calculated the ordinary least squares estimate for flowering time, seed mass, and tiller number as well as for seven additional traits recorded in the physiology and growth chamber experiments. We excluded total plant biomass from the set of predictors because biomass and seed number are tightly correlated (>0.9). For similar reasons, we also excluded the height of the largest inflorescence (Inflorescence(h)). The posterior mean and 90% credible intervals of selection coefficients are given in Figure 6.

Late flowering was generally associated with greater fitness at cool and wet sites (i.e. Sheep Station and Cheyenne), whereas early flowering led to greater fitness at dry and/or hot sites (i.e. Baltzor and Wildcat). Early flowering was also associated with higher fitness in the growth chamber, the hottest environment on average. Genotypes that produced larger seeds generally had lower fitness, although larger seeds were associated with greater reproductive success in the low-density treatments of Sheep Station. Evidence of selection for tiller number was strong and more tillers was consistently associated with higher fitness. Greater decreases in Fv/Fm, the efficiency of Photosystem II, post-freezing (a measure of freezing intolerance) were associated with lower fitness at Baltzor, the coldest environment on average. We assessed the predictive performance of our KO model relative to existing ordination/latent variable models in a cross-validation study. We partitioned the data from each experiment into 10 random folds. Each fold retained 90% observations for model fitting and 10% for out-of-sample prediction. We excluded the MMM from the cross-validation study because of severe computational burden (runtime ≈2 days for a single fold).

All ordination methods were slightly conservative with coverage near 1 for each trait (Figure 7). As in the simulation study, the unconstrained ordination model serves as a baseline for quantifying gains in predictive performance associated with accounting for environmental associations and kinship. For traits recorded in the common garden and physiology experiments (i.e. FT to SLA), accounting for environmental associations generally decreased bias and variability in the posterior predictive distributions. One exception was for the trait Phenological, for which all models resulted in poor predictive performance. Unsurprisingly, environmental associations did not improve prediction for Height, Growth, Leaves(n) and Inflorescence(h)

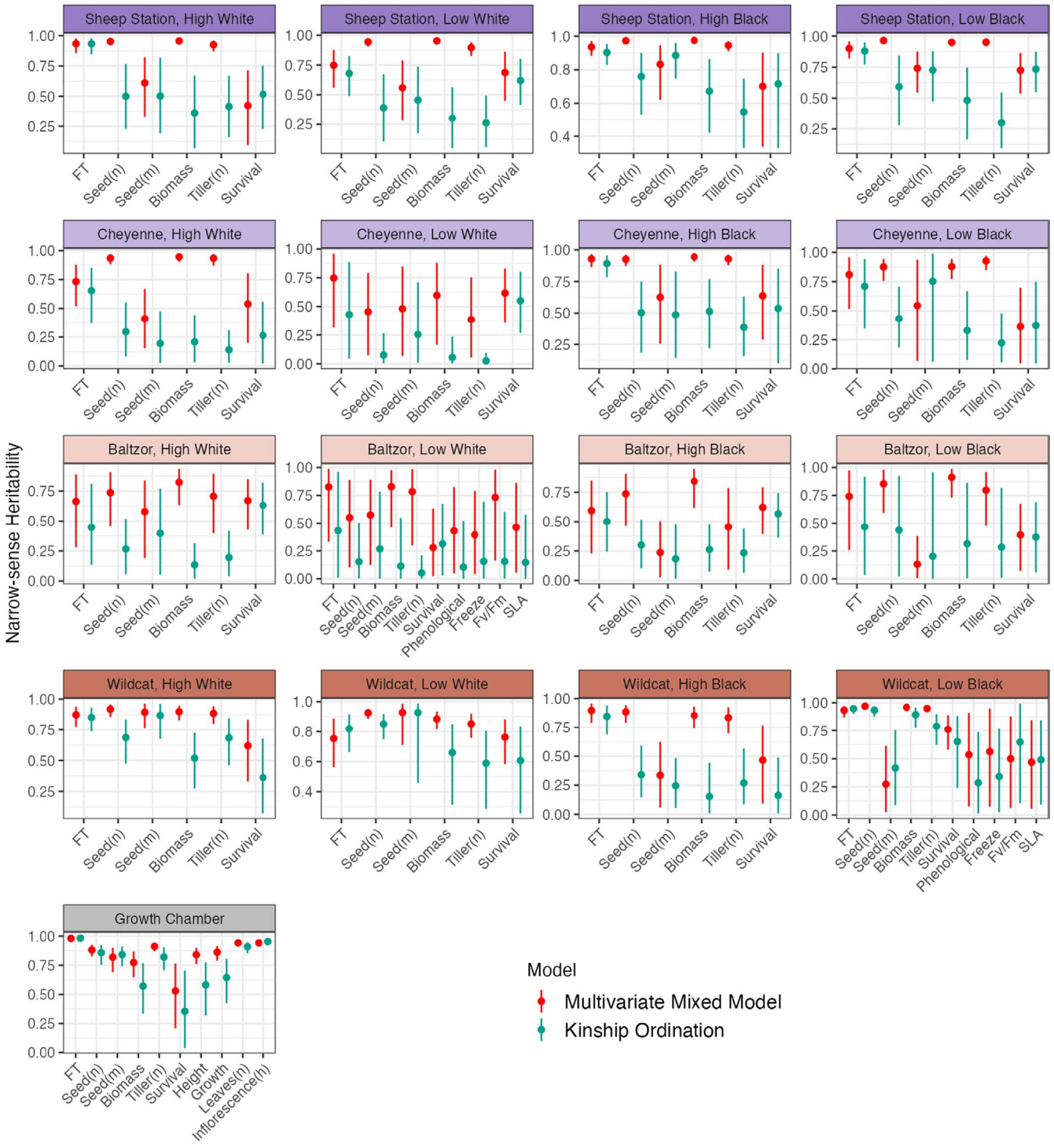



FIGURE 5 Heritability of 14 traits measured across 17 environments. Posterior means along with 90% credible intervals displayed for multivariate mixed modelling and kinship ordination approaches. Trait descriptions are provided in the Supporting Information. Sites are ordered from top to bottom from least to most hot and dry based on principal components analysis for various bioclimatic variables. 'Low' and 'High' abbreviate low density and high density intraspecific competition treatments (Figure 1), respectively. 'White' and 'Black' abbreviate low (white gravel) and high (black gravel) temperature treatments, respectively.

because these traits were only recorded in the growth chamber. Accounting for kinship, as in our KO model, decreased bias and variability for most traits but not those recorded in the physiology study (i.e. Survival, Freeze, Fv/Fm, SLA). Note the estimated heritability of these traits was low (Figure 5), so that variation in trait values did not correlate with kinship. In contrast, accounting for kinship substantially improved prediction for FT, Survival, Leaves(n), and Inflorescence(h), which had some of the highest heritability estimates (Figure 5). Accounting for kinship also increased computational burden.

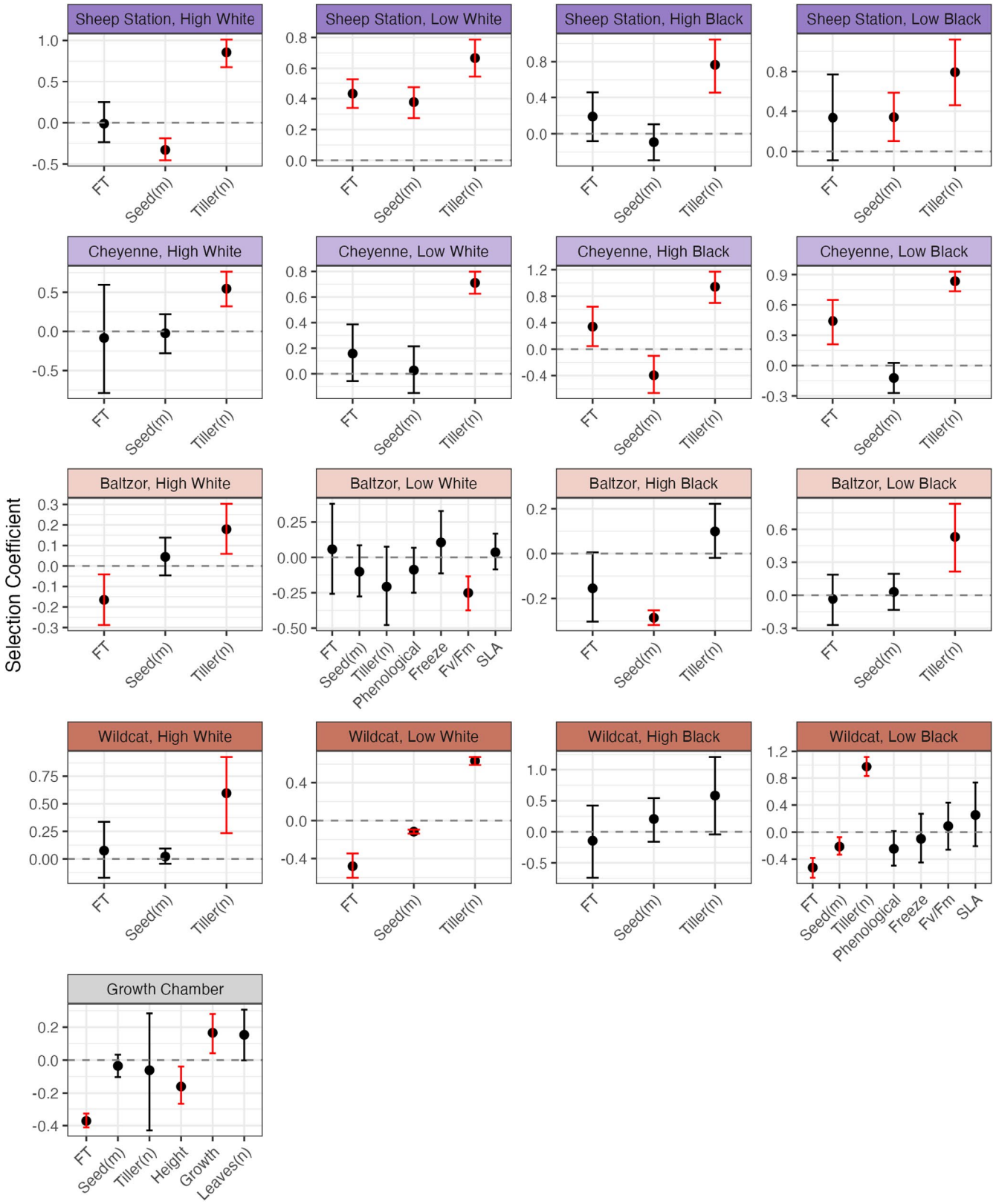



FIGURE 6 Selection coefficient posterior means and 90% credible intervals. Red intervals exclude 0 and indicate traits under selection. Sites are ordered from top to bottom from least to most hot and dry. 'Low' and 'High' abbreviate low density and high density intraspecific competition treatments (Figure 1), respectively. 'White' and 'Black' abbreviate white gravel and black gravel temperature treatments, respectively. The grey horizontal dashed lines indicate $y = 0$.




**FIGURE 7** Out-of-sample predictive performance for 14 *B. tectorum* traits. Boxplots summarize the predictive performance for each genotype averaged across all environments in which the trait was measured. Note that this is one environment for traits Growth, Height, Infloresence(h), and Leaves(n) and two environments for traits Phenological, Freeze, Fv/Fm, and SLA. Trait descriptions are provided in the Supporting Information.

## 5 | DISCUSSION

Latent variable models have become a popular approach for parsimoniously incorporating correlation in high-dimensional data (Doser et al., 2025; Hui et al., 2015; Stein, 2014; van der Veen et al., 2023; Warton et al., 2015; Wright et al., 2025; Yee, 2004). Model parsimony has implications for computation, prediction, and inference. Fewer parameters reduces computing time (McGillycuddy et al., 2025) and the potential for convergence issues, which are frequently encountered when fitting mixed models (Ahlinder et al., 2024; Ahlinder & Sillanpää, 2013). Parsimony can facilitate prediction through regularization (Hooten & Hobbs, 2015; Stein, 2014). Regularization also induces parameter bias but reduces variance, which may be a helpful trade-off, especially when analysing sparse datasets. We have proposed application of latent variable models to sparse, multi-trait data to jointly estimate heritability and environmental associations in experiments where not all traits are measured in each environment. In this context, standard multivariate mixed model are not directly applicable and must be fit to subsets of the data independently. More generally, we have proposed modelling the latent variables using a proportional covariance structure, which can improve prediction and parameter estimation when trait variation is well approximated by the kinship matrix.

In the simulation study, we assessed the validity of using our KO approach to facilitate posterior inference and prediction from complete datasets (i.e. all traits measured in each environment) simulated from a multivariate mixed model. We found that our KO approach provided similar performance to the MMM used to simulate the data but reduced computational burden by an order of magnitude. The drawbacks of applying our KO approach were relatively mild and included slightly lower coverage and elevated bias for heritability and environmental associations relative to the MMM. The two approaches resulted in identical predictive performance.

More broadly, we quantified the advantages of incorporating genomic information into commonly applied ordination and latent variable models in ecology. In addition to facilitating posterior inference for heritability, accounting for genomic structure in the covariance of latent variables also improved coverage for covariate associations, $\boldsymbol{\beta}$. We found that ignoring kinship in ordination methods resulted in overly narrow posterior distributions for $\boldsymbol{\beta}$. Treating genotypes independently leads to overconfidence, a consequence analogous to ignoring spatial dependence when estimating $\boldsymbol{\beta}$ in spatial generalized linear mixed models (Hanks et al., 2015; Khan & Calder, 2022; Zimmerman & Ver Hoef, 2022). Incorporating kinship within latent variable models can also improve prediction, especially for traits with high heritability, as we found in the cross-validation analysis.

Unlike standard mixed models, our KO approach can be used to obtain joint inference when the collection of traits recorded differs by environment. In the data reconciliation analysis of *B. tectorum*,

analysing the full dataset increased the precision of heritability estimates for physiological traits that were recorded for a reduced number of genotypes and environments. Our KO approach also facilitated model parsimony and resulted in more biologically reasonable estimates of heritability. The heritability estimates associated with the MMM were near 1 for production-related traits. In mixed models, trait variation is decomposed into genetic $\zeta^2$ and error $\sigma^2$ variance components, and such high heritability estimates correspond to near-zero error variances. These unrealistic estimates may be related to the tendency of linear mixed models to estimate variance–covariance parameters at the boundary of the parameter space when the data are insufficiently informative, a drawback noted for both frequentist (Bolker et al., 2009) and Bayesian (Gelman, 2006) implementations. Our KO approach may stabilize inference by increasing the ratio of data to parameters through data integration (i.e. joint analysis of all traits) and reducing model complexity via latent variables.

While we have motivated our KO approach in the context of varying trait collections across environments, we caution against implementing our model for experiments where two or more environments have no recorded traits in common. It would not be advisable to fit our model to the physiology study traits in the absence of overlapping measurements from the six traits (i.e. FT, Seed(n), Seed(m), Biomass, Tiller(n) and Survival) measured in all environments. These traits provide reproducibility for estimation of the low-rank covariate associations (i.e. $\boldsymbol{\beta}_l$). The motivation for our framework is that the additional traits measured in specific environments can be approximated by latent variables that are primarily a function of the most commonly collected traits.

The trait selection analysis corroborates previous analyses documenting varying life-history strategies across *B. tectorum* populations. Strategies appear to focus on drought escape and follow a continuum from slow to fast. Early flowering was associated with higher fitness in hot and dry environments but low fitness in cool and wet climates. Early phenology in desert environments allows *B. tectorum* to complete its life cycle in spring and avoid droughts during summer (Kooyers, 2015; Leger et al., 2009; Rice et al., 1992). On the other hand, later phenology improved fitness in cool and wet environments. The consistency in selection coefficients along this gradient emphasizes the importance of flowering time for shaping reproductive success in diverse environments as well as the high heritability of flowering time (Figure 5).

While selection in flowering time matched environmental gradients, the pattern of selection on seed mass was less obvious. Previous studies have suggested larger seeds may maximize reproductive success per seed in desert environments (Tremayne & Richards, 2000) by allowing plants to speed up their lifecycle and minimize the production of additional non-reproductive tissue. We did not find evidence for this pattern. Larger seeds were primarily associated with lower fitness, although positive associations were observed for the low density treatments of Sheep Station. Flowering time and seed mass were strongly correlated, and one explanation could be that the associations between seed mass and reproductive success along the moisture temperature continuum were obscured by selection on flowering time, the most heritable trait (Figure 5). Seed mass can also improve survival by providing additional nutrients during germination. This resource buffer is thought to be especially important in climates with high-temperature seasonality as *B. tectorum* germinates in late fall or early winter. Related arguments apply to freezing tolerance, which can protect the photosynthetic efficiency of early flowering genotypes in desert environments, which may explain the selection on Fv/Fm at Baltzor (a mid-elevation, cold semi-arid environment).

Tiller formation occurs in the early stages of plant development and can increase reproductive success if resources are sufficient for all tillers to develop inflorescences. However, in water-limited environments, some tillers may senesce before developing inflorescences and decrease resources for the developing reproductive structures on the remaining tillers (Kebrom et al., 2013). The significance of this trade-off can be seen in drought resistant lines of cereal crops that have been selected for fewer tillers (Rasmusson, 1991). In our experiment, selection on tiller number did not align with the climate gradient depicted by the first principal component. More tillers increased reproductive success at all sites. Because the advantage of tillers is related to water availability in a narrow temporal window, long-term climatic patterns as depicted by the top two principal components of the bioclimatic variables likely did not reflect the environmental factors driving reproductive success at these four particular sites in 2022. The lack of congruence with climate gradients in tiller number could also relate to the fact that, like seed mass, tiller number is less heritable than flowering time, which attenuated responses to selection.

Although our KO approach was motivated by improving computational feasibility in multi-trait experiments, the flexibility, scalability, and generality of our model make it straightforward to customize for other datasets and analyses. Our approach is directly applicable to multi-trait multi-environment trials in agronomy. We could account for dominant and epistatic genetic effects and facilitate estimation of broad-sense heritability by augmenting the covariance structure of the latent variables. More broadly, our work complements the existing latent variable modelling literature by highlighting the inferential advantages of incorporating genomic structure within the covariance of the latent variables. While our analysis was primarily retrospective, focusing on the development of clines and life-history trade-offs in *B. tectorum*, our KO approach may also have implications for ecological forecasting, where population responses to novel environments remain difficult to predict (Zipkin & Doser, 2024). If combined with temporally structured data on species occurrence and genomics, a trait-based distribution model could be used to explore forecasts of dispersal and evolutionary change by accounting for trait plasticity and heritability. Such applications would require additional assumptions about the temporal stability of heritability and trait–environment associations but may be valuable for understanding future invasion dynamics of *B. tectorum* under climate change in the Intermountain West.

## AUTHOR CONTRIBUTIONS

Justin J. Van Ee and Mevin B. Hooten developed the statistical methods used in the study. Megan L. Vahsen, Diana Gamba, Toby M. Maxwell, Bill E. Davidson, Brynne E. Lazarus, Lauren M. Porensky, Ruth Hufbauer, Matthew J. Germino, Peter B. Adler and Jesse R. Lasky contributed data and designed the experiments associated with the *B. tectorum* analysis. Justin J. Van Ee and Mevin B. Hooten drafted the manuscript with substantial feedback from all other authors.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210x.70284.

## DATA AVAILABILITY STATEMENT

The data and corresponding `R` and `Stan` scripts used for analysis are available on GitHub and archived at Zenodo (Van Ee, 2026): https://doi.org/10.5281/zenodo.18665916.

## STATEMENT OF INCLUSION

Data analysed in this manuscript were provided by the BromeCast research network: https://bromecast.wixsite.com/home. The network includes more than 40 participants representing universities, NGOs and government research and land management agencies across the United States and Canada. All members were invited to contribute to this manuscript as co-authors.

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## REFERENCES

Ahlinder, J., Hall, D., Suontama, M., & Sillanpää, M. J. (2024). Principal component analysis revisited: Fast multitrait genetic evaluations with smooth convergence. *G3 (Bethesda, Md.)*, *14*, jkae228.

Ahlinder, J., & Sillanpää, M. J. (2013). Rapid Bayesian inference of heritability in animal models without convergence problems. *Methods in Ecology and Evolution*, *4*, 1037–1046.

Andrés, F., & Coupland, G. (2012). The genetic basis of flowering responses to seasonal cues. *Nature Reviews Genetics*, *13*, 627–639.

Azevedo, C. F., Barreto, C. A. V., Nascimento, M., Carvalho, I. R., Kehl, K., Cruz, C. D., & Nascimento, A. C. C. (2023). Genotype-by-environment interaction of wheat using Bayesian factor analytic models and environmental covariates. *Euphytica*, *219*, 95.

Balch, J. K., Bradley, B. A., D'Antonio, C. M., & Gómez-Dans, J. (2013). Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). *Global Change Biology*, *19*, 173–183.

Bartholomew, D. J., Knott, M., & Moustaki, I. (2011). *Latent variable models and factor analysis: A unified approach*. John Wiley & Sons.

Bauer, A., Hoti, F., Reetz, T., Schuh, W.-D., Léon, J., & Sillanpää, M. (2009). Bayesian prediction of breeding values by accounting for genotype-by-environment interaction in self-pollinating crops. *Genetical Research*, *91*, 193–207.

Bhattacharya, A., & Dunson, D. B. (2011). Sparse Bayesian infinite factor models. *Biometrika*, *98*, 291–306.

Bogdan, M., Chakrabarti, A., Frommlet, F., & Ghosh, J. K. (2011). Asymptotic Bayes-optimality under sparsity of some multiple testing procedures. *Annals of Statistics*, *39*, 1551–1579.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*, 127–135.

Broman, K. W., Gatti, D. M., Simecek, P., Furlotte, N. A., Prins, P., Sen, Ś., Yandell, B. S., & Churchill, G. A. (2019). `R/qtl2`: Software for mapping quantitative trait loci with high-dimensional data and multiparent populations. *Genetics*, *211*, 495–502.

Brooks, M. E., Bolker, B., Kristensen, K., Maechler, M., Magnusson, A., McGillycuddy, M., Skaug, H., Nielsen, A., Berg, C., van Benthem, K., Sadat, N., Lüdecke, D., Lenth, R., O'Brien, J., Geyer, C. J., Jagan, M., Wiernik, B., Stouffer, D. B., Agronah, M., … Williams, C. (2026). glmmTMB: Generalized linear mixed models using template model builder. R package version 1.1.14.

Brooks, M. L., D'antonio, C. M., Richardson, D. M., Grace, J. B., Keeley, J. E., Ditomaso, J. O. S. E. P. H. M., Hobbs, R. I. C. H. A. R. D. J., Pellant, M. I. K. E., & Pyke, D. A. V. I. D. (2004). Effects of invasive alien plants on fire regimes. *Bioscience*, *54*, 677–688.

Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., & Riddell, A. (2017). Stan: A probabilistic programming language. *Journal of Statistical Software*, *76*, 1–32.

Carvalho, C. M., Polson, N. G., & Scott, J. G. (2010). The horseshoe estimator for sparse signals. *Biometrika*, *97*, 465–480.

Cattell, R. B. (1966). The scree test for the number of factors. *Multivariate Behavioral Research*, *1*, 245–276.

Clark, N. J., & Wells, K. (2023). Dynamic generalised additive models (DGAMs) for forecasting discrete ecological time series. *Methods in Ecology and Evolution*, *14*, 771–784.

Covarrubias-Pazaran, G. (2018). Software update: Moving the R package sommer to multivariate mixed models for genome-assisted prediction. *bioRxiv*. https://doi.org/10.1101/354639

Davies, P., & Tso, M. K. (1982). Procedures for reduced-rank regression. *Applied Statistics*, *31*, 244–255.

de Villemereuil, P., Gaggiotti, O. E., Mouterde, M., & Till-Bottraud, I. (2016). Common garden experiments in the genomic era: New perspectives and opportunities. *Heredity*, *116*, 249–254.

Doser, J. W., Finley, A. O., Saunders, S. P., Kéry, M., Weed, A. S., & Zipkin, E. F. (2025). Modeling complex species-environment relationships through spatially-varying coefficient occupancy models. *Journal of Agricultural, Biological and Environmental Statistics*, *30*, 146–171.

Endelman, J. B. (2011). Ridge regression and other kernels for genomic selection with `R` package `rrBLUP`. *The Plant Genome*, *4*, 250–255.

Endelman, J. B. (2023). Fully efficient, two-stage analysis of multi-environment trials with directional dominance and multi-trait genomic selection. *Theoretical and Applied Genetics*, *136*, 65.

Gamba, D., Vahsen, M. L., Maxwell, T. M., Pirtel, N., Romero, S., Van Ee, J. J., Penn, A., Das, A., Ben-Zeev, R., Baughman, O., Blaney, C. S., Bodkins, R., Budha-Magar, S., Copeland, S. M., Davis-Foust, S. L., Diamond, A., Donnelly, R. C., Dunwiddie, P. W., Ensing, D. J., … Lasky, J. R. (2025). Local adaptation to climate has facilitated the global invasion of cheatgrass. *Nature Communications*, *16*, 10203.

Gelfand, A. E., & Smith, A. F. (1990). Sampling-based approaches to calculating marginal densities. *Journal of the American Statistical Association*, *85*, 398–409.

Gelman, A. (2006). Prior distributions for variance parameters in hierarchical models (comment on article by Browne and Draper). *Bayesian Analysis*, *1*, 515–534.

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, *7*, 457–472.

Germino, M. J., Chambers, J. C., & Brown, C. S. (2016). *Exotic brome-grasses in arid and semiarid ecosystems of the Western US*. Springer.

Geweke, J., & Zhou, G. (1996). Measuring the pricing error of the arbitrage pricing theory. *The Review of Financial Studies*, *9*, 557–587.

Geyer, C. J. (1992). Practical Markov chain Monte Carlo. *Statistical Science*, *7*, 473–483.

Gill, H. S., Halder, J., Zhang, J., Brar, N. K., Rai, T. S., Hall, C., Bernardo, A., Amand, P. S., Bai, G., Olson, E., Ali, S., Turnipseed, B., & Sehgal, S. K. (2021). Multi-trait multi-environment genomic prediction of agronomic traits in advanced breeding lines of winter wheat. *Frontiers in Plant Science*, *12*, 709545.

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, *33*, 1–22.

Hallander, J., Waldmann, P., Wang, C., & Sillanpaa, M. J. (2010). Bayesian inference of genetic parameters based on conditional decompositions of multivariate normal distributions. *Genetics*, *185*, 645–654.

Hanks, E. M., Hooten, M. B., & Baker, F. A. (2011). Reconciling multiple data sources to improve accuracy of large-scale prediction of forest disease incidence. *Ecological Applications*, *21*, 1173–1188.

Hanks, E. M., Schliep, E. M., Hooten, M. B., & Hoeting, J. A. (2015). Restricted spatial regression in practice: Geostatistical models, confounding, and robustness under model misspecification. *Environmetrics*, *26*, 243–254.

He, D., Kuhn, D., & Parida, L. (2016). Novel applications of multitask learning and multiple output regression to multiple genetic trait prediction. *Bioinformatics*, *32*, 37–43.

Henderson, C. R. (1975). Best linear unbiased estimation and prediction under a selection model. *Biometrics*, *31*, 423–447.

Hill, W. G., Goddard, M. E., & Visscher, P. M. (2008). Data and theory point to mainly additive genetic variance for complex traits. *PLoS Genetics*, *4*, e1000008.

Hooten, M. B., & Hobbs, N. T. (2015). A guide to Bayesian model selection for ecologists. *Ecological Monographs*, *85*, 3–28.

Howell, A., Winkler, D. E., Phillips, M. L., McNellis, B., & Reed, S. C. (2020). Experimental warming changes phenology and shortens growing season of the dominant invasive plant *Bromus tectorum* (cheatgrass). *Frontiers in Plant Science*, *11*, 570001.

Huber, P., Ronchetti, E., & Victoria-Feser, M.-P. (2004). Estimation of generalized linear latent variable models. *Journal of the Royal Statistical Society, Series B: Statistical Methodology*, *66*, 893–908.

Hufft, R. A., & Zelikova, T. J. (2016). Ecological genetics, local adaptation, and phenotypic plasticity in *Bromus tectorum* in the context of a changing climate. In *Exotic brome-grasses in arid and semiarid ecosystems of the Western US: Causes, consequences, and management implications*. Springer.

Hui, F. K., Taskinen, S., Pledger, S., Foster, S. D., & Warton, D. I. (2015). Model-based approaches to unconstrained ordination. *Methods in Ecology and Evolution*, *6*, 399–411.

Isik, F., Holland, J., & Maltecca, C. (2017). *Genetic data analysis for plant and animal breeding*. Springer.

Ives, A. R. (2015). For testing the significance of regression coefficients, go ahead and log-transform count data. *Methods in Ecology and Evolution*, *6*, 828–835.

Johnstone, I. M., & Titterington, D. M. (2009). Statistical challenges of high-dimensional data. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, *367*, 4237–4253.

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the Earth's land surface areas. *Scientific Data*, *4*, 1–20.

Kebrom, T. H., Spielmeyer, W., & Finnegan, E. J. (2013). Grasses provide new insights into regulation of shoot branching. *Trends in Plant Science*, *18*, 41–48.

Khan, K., & Calder, C. A. (2022). Restricted spatial regression methods: Implications for inference. *Journal of the American Statistical Association*, *117*, 482–494.

Kooyers, N. J. (2015). The evolution of drought escape and avoidance in natural herbaceous populations. *Plant Science*, *234*, 155–162.

Korhonen, P., Hui, F. K., Niku, J., Taskinen, S., & van der Veen, B. (2025). Gllvm 2.0: Fast fitting of advanced ordination methods and joint species distribution models. *PeerJ*, *13*, e20338.

Kruuk, L. E. (2004). Estimating genetic parameters in natural populations using the 'animal model'. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *359*, 873–890.

Lande, R. (1979). Quantitative genetic analysis of multivariate evolution, applied to brain: Body size allometry. *Evolution*, *33*, 402–416.

Lande, R., & Arnold, S. J. (1983). The measurement of selection on correlated characters. *Evolution*, *37*, 1210–1226.

Lee, S. H., & Van der Werf, J. H. (2016). MTG2: An efficient algorithm for multivariate linear mixed model analysis based on genomic information. *Bioinformatics*, *32*, 1420–1422.

Leger, E. A., Espeland, E. K., Merrill, K. R., & Meyer, S. E. (2009). Genetic variation and local adaptation at a cheatgrass (*Bromus tectorum*) invasion edge in western Nevada. *Molecular Ecology*, *18*, 4366–4379.

Lewandowski, D., Kurowicka, D., & Joe, H. (2009). Generating random correlation matrices based on vines and extended onion method. *Journal of Multivariate Analysis*, *100*, 1989–2001.

Li, S., Lu, S., Wang, J., Chen, Z., Zhang, Y., Duan, J., Liu, P., Wang, X., & Guo, J. (2023). Responses of physiological, morphological and anatomical traits to abiotic stress in woody plants. *Forests*, *14*, 1784.

Little, R. J. (2006). Calibrated Bayes: A Bayes/frequentist roadmap. *The American Statistician*, *60*, 213–223.

Lynch, M., Walsh, B., et al. (1998). *Genetics and analysis of quantitative traits*. Sinauer Sunderland.

Mack, R. N. (1981). Invasion of *Bromus tectorum* l. into Western North America: An ecological chronicle. *Agro-Ecosystems*, *7*, 145–165.

Mathew, B., Bauer, A., Koistinen, P., Reetz, T., Léon, J., & Sillanpää, M. (2012). Bayesian adaptive Markov chain Monte Carlo estimation of genetic parameters. *Heredity*, *109*, 235–245.

Maxwell, T. M., Germino, M. J., Romero, S., Porensky, L. M., Blumenthal, D. M., Brown, C. S., & Adler, P. B. (2023). Experimental manipulation of soil-surface albedo alters phenology and growth of *Bromus tectorum* (Cheatgrass). *Plant and Soil*, *487*, 325–339.

McGillycuddy, M., Popovic, G., Bolker, B. M., & Warton, D. I. (2025). Parsimoniously fitting large multivariate random effects in glmmTMB. *Journal of Statistical Software*, *112*, 1–19.

Meyer, K. (2007). Multivariate analyses of carcass traits for Angus cattle fitting reduced rank and factor analytic models. *Journal of Animal Breeding and Genetics*, *124*, 50–64.

Misztal, I. (2008). Reliable computing in estimation of variance components. *Journal of Animal Breeding and Genetics*, *125*, 363–370.

Montesinos-López, O. A., Montesinos-López, A., Crossa, J., Toledo, F. H., Pérez-Hernández, O., Eskridge, K. M., & Rutkoski, J. (2016). A genomic Bayesian multi-trait and multi-environment model. *G3: Genes, Genomes, Genetics*, *6*, 2725–2744.

Niku, J., Brooks, W., Herliansyah, R., Hui, F. K. C., Korhonen, P., Taskinen, S., van der Veen, B., & Warton, D. I. (2025). gllvm: Generalized linear latent variable models. R package version 2.0.5.

Niku, J., Hui, F. K., Taskinen, S., & Warton, D. I. (2019). Gllvm: Fast analysis of multivariate abundance data with generalized linear latent variable models in R. *Methods in Ecology and Evolution*, *10*, 2173–2182.

Oba, S., Sato, M.-a., Takemasa, I., Monden, M., Matsubara, K.-i., & Ishii, S. (2003). A Bayesian missing value estimation method for gene expression profile data. *Bioinformatics*, *19*, 2088–2096.

O'Hara, R., & Kotze, J. (2010). Do not log-transform count data. *Methods in Ecology and Evolution*, *1*, 118–122.

O'Hara, R., & Van Der Veen, B. (2024). Hierarchical ordination, a unifying framework for drivers of community processes. *bioRxiv*, 574701.

Ovaskainen, O., Tikhonov, G., Norberg, A., Guillaume Blanchet, F., Duan, L., Dunson, D., Roslin, T., & Abrego, N. (2017). How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters*, *20*, 561–576.

Papastamoulis, P., & Ntzoufras, I. (2022). On the identifiability of Bayesian factor analytic models. *Statistics and Computing*, *32*, 23.

Pérez, P., & de Los Campos, G. (2014). Genome-wide regression and prediction with the `BGLR` statistical package. *Genetics*, *198*, 483–495.

Pichler, M., & Hartig, F. (2021). A new joint species distribution model for faster and more accurate inference of species associations from big community data. *Methods in Ecology and Evolution*, *12*, 2159–2173.

Pollak, E., der Van Werf, J., & Quaas, R. (1984). Selection bias and multiple trait evaluation. *Journal of Dairy Science*, *67*, 1590–1595.

Pollock, L. J., Tingley, R., Morris, W. K., Golding, N., O'Hara, R. B., Parris, K. M., Vesk, P. A., & McCarthy, M. A. (2014). Understanding co-occurrence by modelling species simultaneously with a joint species distribution model (JSDM). *Methods in Ecology and Evolution*, *5*, 397–406.

Popovic, G. C., Hui, F. K., & Warton, D. I. (2022). Fast model-based ordination with copulas. *Methods in Ecology and Evolution*, *13*, 194–202.

R Core Team. (2024). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rasmusson, D. (1991). A plant breeder's experience with ideotype breeding. *Field Crops Research*, *26*, 191–200.

Rice, K., Black, R., Radamaker, G., & Evans, R. (1992). Photosynthesis, growth, and biomass allocation in habitat ecotypes of cheatgrass (*Bromus tectorum*). *Functional Ecology*, *6*, 32–40.

Robinson, P. M. (1973). Generalized canonical analysis for time series. *Journal of Multivariate Analysis*, *3*, 141–160.

Sandhu, K. S., Patil, S. S., Aoun, M., & Carter, A. H. (2022). Multi-trait multi-environment genomic prediction for end-use quality traits in winter wheat. *Frontiers in Genetics*, *13*, 831020.

Schielzeth, H., Dingemanse, N. J., Nakagawa, S., Westneat, D. F., Allegue, H., Teplitsky, C., Réale, D., Dochtermann, N. A., Garamszegi, L. Z., & Araya-Ajoy, Y. G. (2020). Robustness of linear mixed-effects models to violations of distributional assumptions. *Methods in Ecology and Evolution*, *11*, 1141–1152.

Schulthess, A. W., Zhao, Y., Longin, C. F. H., & Reif, J. C. (2018). Advantages and limitations of multiple-trait genomic prediction for Fusarium head blight severity in hybrid wheat (*Triticum aestivum* l.). *Theoretical and Applied Genetics*, *131*, 685–701.

Schwinning, S., Lortie, C. J., Esque, T. C., & DeFalco, L. A. (2022). What common-garden experiments tell us about climate responses in plants. *Journal of Ecology*, *110*, 986–996.

Sillanpää, M. J. (2011). On statistical methods for estimating heritability in wild populations. *Molecular Ecology*, *20*, 1324–1332.

Stan Development Team. (2024). *Stan user's guide*.

Stein, M. L. (2014). Limitations on low rank approximations for covariance matrices of spatial data. *Spatial Statistics*, *8*, 1–19.

Tibshirani, R. (1996). Regression shrinkage and selection via the lasso. *Journal of the Royal Statistical Society, Series B: Statistical Methodology*, *58*, 267–288.

Tikhonov, G., Opedal, Ø. H., Abrego, N., Lehikoinen, A., de Jonge, M. M., Oksanen, J., & Ovaskainen, O. (2020). Joint species distribution modelling with the R-package Hmsc. *Methods in Ecology and Evolution*, *11*, 442–447.

Tipping, M. E., & Bishop, C. M. (1999). Probabilistic principal component analysis. *Journal of the Royal Statistical Society, Series B: Statistical Methodology*, *61*, 611–622.

Tipton, J., Hooten, M., & Goring, S. (2017). Reconstruction of spatio-temporal temperature from sparse historical records using robust probabilistic principal component regression. *Advances in Statistical Climatology, Meteorology and Oceanography*, *3*, 1–16.

Tredennick, A. T., Hooker, G., Ellner, S. P., & Adler, P. B. (2021). A practical guide to selecting models for exploration, inference, and prediction in ecology. *Ecology*, *102*, e03336.

Tremayne, M. A., & Richards, A. (2000). Seed weight and seed number affect subsequent fitness in outcrossing and selfing *Primula* species. *New Phytologist*, *148*, 127–142.

Vahsen, M., Maxwell, T., Blumenthal, D., Gamba, D., Germino, M., Hooten, M., Lasky, J. R., Leger, E. A., Pirtel, N., Porensky, L. M., Romero, S., Van Ee, J. J., Copeland, S. M., Ensing, D. J., & Adler, P. B. (2025). Phenological responses of *Bromus tectorum* genotypes depends on current and source environments. *Ecology*, *106*, e70025.

Van der Sluis, S., Posthuma, D., & Dolan, C. V. (2013). `TATES`: Efficient multivariate genotype-phenotype analysis for genome-wide association studies. *PLoS Genetics*, *9*, e1003235.

van der Veen, B., Hui, F. K., Hovstad, K. A., & O'Hara, R. B. (2023). Concurrent ordination: Simultaneous unconstrained and constrained latent variable modelling. *Methods in Ecology and Evolution*, *14*, 683–695.

van der Veen, B., Hui, F. K., Hovstad, K. A., Solbu, E. B., & O'Hara, R. B. (2021). Model-based ordination for species with unequal niche widths. *Methods in Ecology and Evolution*, *12*, 1288–1300.

van der Veen, B., & O'Hara, R. B. (2024). Fast fitting of phylogenetic mixed-effects models. arXiv, 2408.05333.

Van Ee, J. (2026). Data and code for "Data reconciliation in multi-trait experiments with kinship ordination".

Waldmann, P., Hallander, J., Hoti, F., & Sillanpaa, M. J. (2008). Efficient Markov chain Monte Carlo implementation of Bayesian analysis of additive and dominance genetic variances in noninbred pedigrees. *Genetics*, *179*, 1101–1112.

Warton, D., Blanchet, F. G., O'Hara, R., Ovaskainen, O., Taskinen, S., Walker, S., Warton, D. I., O'Hara, R. B., Walker, S. C., & Hui, F. K. C. (2015). So many variables: Joint modeling in community ecology. *Trends in Ecology & Evolution*, *30*, 766–779.

Warton, D. I., Lyons, M., Stoklosa, J., & Ives, A. R. (2016). Three points to consider when choosing a LM or GLM test for count data. *Methods in Ecology and Evolution*, *7*, 882–890.

Wilkinson, D. P., Golding, N., Guillera-Arroita, G., Tingley, R., & McCarthy, M. A. (2019). A comparison of joint species distribution models for presence–absence data. *Methods in Ecology and Evolution*, *10*, 198–211.

Wilson, A. J., Réale, D., Clements, M. N., Morrissey, M. M., Postma, E., Walling, C. A., Kruuk, L. E. B., & Nussey, D. H. (2010). An ecologist's guide to the animal model. *Journal of Animal Ecology*, *79*, 13–26.

Wright, W. J., Neitlich, P. N., & Hooten, M. B. (2025). Clipped multiscale spatial processes for multivariate plant cover data. *The Annals of Applied Statistics*, *19*, 2918–2936.

Yee, T. W. (2004). A new technique for maximum-likelihood canonical Gaussian ordination. *Ecological Monographs*, *74*, 685–701.

Zheng, X., Levine, D., Shen, J., Gogarten, S. M., Laurie, C., & Weir, B. S. (2012). A high-performance computing toolset for relatedness and principal component analysis of SNP data. *Bioinformatics*, *28*, 3326–3328.

Zimmerman, D. L., & Ver Hoef, J. M. (2022). On deconfounding spatial confounding in linear models. *The American Statistician*, *76*, 159–167.

Zipkin, E. F., & Doser, J. W. (2024). Context matters in ecological forecasting: Lessons in predicting species distributions. *Global Change Biology*, *30*, e17123.

Zipkin, E. F., Zylstra, E. R., Wright, A. D., Saunders, S. P., Finley, A. O., Dietze, M. C., Itter, M. S., & Tingley, M. W. (2021). Addressing data integration challenges to link ecological processes across scales. *Frontiers in Ecology and the Environment*, *19*, 30–38.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**S1.** Specification of prior distributions, mathematical details related to identifiability of factor matrix, and description of *Bromus tectorum* experiments.

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