

Modelling the Coexistence of Phenotypic Plasticity and Habitat Choice Using a Simulation Based Approach

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Abstract

This study explores the performance of double hierarchical Bayesian models in estimating trait-habitat relationships, looking at plasticity in response to habitat variation and habitat selection as a non-random process. Using a simulation-based approach, we simulated datasets following a structured causal process, linking habitat choice and environmental plasticity, then evaluated the performance of four distinct statistical models: a univariate model of a plastic trait, a bivariate model of habitat and trait, a bivariate model including habitat and trait specialization, and a causal structure model explicitly modelling the causal relation between habitat choice and plasticity in a trait. We simulated three hundred datasets for three different sampling schemes with different numbers of individuals and repeated measurements per individual. We estimated bias and precision of estimates for each model. Results indicate that the causal model consistently outperforms all other models in this scenario. Bivariate models tended to over or underestimate the parameters, whereas the univariate model overestimated the role of plasticity in individual variation. As expected, larger sample sizes improved both precision and accuracy of estimates. The insights gained from this simulation study inform the selection and application of statistical methods for studying individual variation in traits in ecological research.

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Introduction

Habitat plays a central role in the ecology and evolution of living organisms, influencing their survival, reproduction, and ultimately their fitness (Edelaar et al. 2008). The concept of habitat has been defined and conceptualized in various ways, depending on the research objectives and the level of biological organization under study. Definitions range from broad, community-level descriptions to specific, species or individual centered perspectives that recognize habitat choice as an important behavioral process (Kirk et al. 2018). From a species centered perspective, habitat has often been defined as a set of environmental conditions, resources, and risks that influence where a species is found. However, such definitions often overlook the fact that individuals within a population can vary in their habitat use, driven by differences in morphology, physiology, behavior, or even prior experience (Montgomery et al. 2018). Furthermore, it needs to be considered that individuals can actively choose their habitats rather than being passively distributed across the landscape (Trappes et al. 2022). These habitat features are what we would like to model along side the trait, as there can be a causal link between the habitat feature an individual has selected, and its phenotype (Regan et al. 2022). To accomplish this, an individual would need to be measured repeatedly for their trait and habitat values, simultaneously, over some period of time.

The recognition that individuals within a population can exhibit variation in habitat use has led to the concept of the individual niche or individual specialization, which emphasizes that habitat use can differ among individuals even within the same population (Wang et al. 2023). This variation can arise from genetic differences, developmental plasticity, or active habitat selection based on individual preferences or performance (Bolnick 2003). Habitat choice, therefore, represents an important dimension of an individual's ecological niche that can contribute to the maintenance of phenotypic diversity within populations.

While habitat choice has been studied extensively in the context of population density, competition, and predation, fewer studies have examined how habitat selection interacts with phenotypic plasticity, another adaptive strategy that individuals use to cope with environmental variability. Phenotypic plasticity allows individuals to modify their phenotype in response to environmental conditions, thereby potentially enhancing fitness across a range of habitats (Reed et al. 2011). However, the extent to which habitat choice and phenotypic plasticity co-evolve and coexist as adaptive strategies within populations remains poorly understood.

Theoretical and empirical studies have begun to address the interplay between habitat choice and phenotypic plasticity. For example, simulation studies have shown that matching habitat choice, where individuals select habitats that best match their phenotype, can outperform phenotypic plasticity under certain conditions (Edelaar et al. 2017, Nicolaus and Edelaar 2018). Other studies have also demonstrated that individuals can vary in their plasticity and habitat choice, suggesting that these strategies may co-exist within populations (Lowe and Addis, 2019). Further, it has been shown that habitat choice can have direct influence on phenotypic plasticity, either by promoting or limiting the effects of plasticity (Turko and Rossi, 2022).

Despite progress in understanding the interactions between plasticity and habitat choice, most studies have focused on population-level differences or assumed that all individuals respond similarly to habitat variation. A more comprehensive framework is needed to account for individual-level differences in plasticity and habitat selection within populations. Such a framework should also allow for the estimation of genetic and environmental variance components associated with these processes.

This study tests a statistical framework, currently being proposed by Patrick et al, that treats an individual's habitat use as an extended phenotype. This allows for the estimation of variance components associated with habitat choice and their covariances with phenotypic traits measured directly on the individual. If we ignore the fact that individuals can actively select their habitat and that phenotypic traits can covary with this habitat selection, we would miss a crucial source of variation when estimating trait values at the individual level (Leclerc et al. 2015). This proposed statistical framework, labeled the causal model, is more complex than the models that are commonly used in trait estimation contexts. For example, consider a population of birds where individuals vary in their boldness, and a habitat feature is measured as proximity to humans. More bold individuals may be willing to nest near human-altered environments, where food is abundant, but disturbance is high, while shy individuals may avoid such areas. Individuals in this hypothetical population will vary, among each other, in their mean values for both the trait and habitat feature. Individuals may also vary in the range of habitat values they occupy. Finally, individuals may vary in their response to changes in the habitat value, and how precise that response is. The values associated with these sources of variation are the parameters we would like to learn and extract from the model. The causal model allows us to explicitly test whether boldness is influenced by the habitat value (plastic response) or if the habitat value is chosen based on the underlying boldness that was already present (matching habitat choice). Both these strategies may be important in maintaining phenotypic variation, in this study we would like to test if the causal model is able to disentangle these sources of variation. Currently the performance of this model is unknown, including the data structure/requirements needed to extract unbiased estimates. In contrast, standard bivariate models can capture correlations between trait and habitat use, but they cannot distinguish whether one trait influences the other or if both are shaped by shared underlying factors. By specifying a directional relationship, the causal model enables clearer

biological interpretation, helping to uncover mechanisms that drive individual differences in habitat strategies rather than describing associations. This approach will provide insights into the coexistence of habitat choice and phenotypic plasticity within populations, and how these strategies contribute to the maintenance of phenotypic variation.

Objectives:

The objective of this study is to evaluate the causal model that was proposed by the framework of treating each individual's selected habitat feature as a trait. This will be done in the context of estimating a specific phenotypic trait at the individual level, where both variation in phenotypic plasticity and habitat choice are contributing to variance in that trait. In total, four models will be tested using a simulation-based approach, three of these models are commonly used, whereas the causal model is not. Each model will be fitted using simulated data and then parameter estimates for fixed and random effects will be extracted. The goal is to determine if the causal model is able to reliably, in a nonbiased manner, estimate the true values for the parameters. Simultaneously, we are interested in seeing how biased, if at all, the simpler models are in terms of their estimates. This process will be repeated with three different sampling structures as we also want to test if the causal model can be accurate given realistic sample sizes. Finally, model metrics will be calculated to determine if the causal model is applicable to biological systems that follow the structure outlined in the simulated data.

Methods

This simulation study assessed the performance of four different models fitted with a Bayesian approach for evaluating variation in trait plasticity and habitat use across individuals. The four models will then be used to estimate the covariances between the

phenotypic trait y and the habitat feature h . Data generation, model fitting and analysis of model metrics were all conducted in R.

Models

Univariate Model: This model estimates the trait y as a function of habitat feature h without explicitly modelling variation in the habitat feature itself. It includes a fixed effect of the habitat on the trait and a random intercept for individuals allowing for deviation away from the mean trait value. Each individual also has a random slope, representing the deviation away from the average slope, representing plasticity. The model assumes that any observed differences in the trait are entirely due to phenotypic plasticity in response to habitat variation. However, since it does not model among-individual variation in habitat selection, it overlooks the possibility that individuals may systematically choose different habitats.

Consequently, it may misattribute habitat-driven variance to trait plasticity. Here y_{ij} is the trait value of individual i at instance j , β_k is the coefficient for fixed effects X_{kij} , α_{y,m_i} is the individual deviation from the mean for trait y and $e_{y_{ij}}$ is the residual deviation for the trait y .

α_{y,p_i} indicates the individual deviation from the average slope β_h representing plasticity,

$$y_{ij} = \sum_k \beta_k X_{kij} + (\beta_h + \alpha_{y,p_i}) h_{ij} + \alpha_{y,m_i} + e_{y_{ij}}$$

Bivariate Model: The bivariate model estimates both the trait y and habitat feature h simultaneously, allowing for the estimation of mean values and variances for each. It partitions total variance into among-individual and within-individual components for both the trait y and the habitat feature h , but does not explicitly model residual variation or variation in plasticity at the individual level. Most notably, this model does not include the random slope for each individual, and assumes that individuals will respond in the same way to habitat variation. Here y_{ij} and h_{ij} are the trait and habitat values of individual i at instance j , β_k and

β_n are the coefficients of fixed effects $X_{k_{ij}}$ and $X_{n_{ij}}$, respectively, α_{y_i} and α_{h_i} are the individual deviations from the mean for the trait y and habitat feature h , and $e_{y_{ij}}$ and $e_{h_{ij}}$ are the residual deviations for the trait y and the habitat feature h .

$$y_{ij} = \sum_k \beta_k X_{k_{ij}} + \alpha_{y_i} + e_{y_{ij}} \quad , \quad h_{ij} = \sum_n \beta_n X_{n_{ij}} + \alpha_{h_i} + e_{h_{ij}}$$

Bivariate Double-Hierarchical Model: This model extends the bivariate model by modelling residual variance for both the trait y and habitat feature h . By estimating residual variation in addition to mean and variance components, this model captures individual differences in the precision of trait responses and habitat use. However, it still lacks a mechanism to model causal relationships between the habitat and the trait, specifically lacking a random slope for each individual. Here γ_l and γ_o are the coefficients of fixed effects for the within-individual residual variance $X_{l_{ij}}$ and $X_{o_{ij}}$, respectively. α_{y,m_i} , α_{h,m_i} , α_{y,v_i} and α_{h,v_i} are the individual deviations from the means (random intercepts) in both trait y and habitat feature h , as well as their residuals.

$$y_{ij} = \sum_k \beta_k X_{k_{ij}} + \alpha_{y,m_i} + e_{y_{ij}} \text{ and } \ln(\sigma_{e_{y_{ij}}}^2) = \sum_l \gamma_l X_{l_{ij}} + \alpha_{y,v_i}$$

$$h_{ij} = \sum_n \beta_n X_{n_{ij}} + \alpha_{h_i} + e_{h_{ij}} \text{ and } \ln(\sigma_{e_{h_{ij}}}^2) = \sum_l \gamma_o X_{o_{ij}} + \alpha_{h,v_i}$$

Causal Model: Here we explicitly model the trait y as a function of habitat feature h while also allowing for random slopes representing variation in individual responses (plasticity). Additionally, it includes residual variance components for both y and h . This model is the most comprehensive, providing accurate partitioning of variance between plasticity, habitat selection, and residual variation. By incorporating a causal structure, it addresses limitations of the previous models by correctly attributing variance to its underlying cause. The equations for the causal model follow the bivariate double hierarchical model with one key addition. Here β_h is the plasticity slope representing the change in trait y as a function of

habitat feature h and α_{y,p_i} is the individual deviation from the average plastic response as a function of h .

$$y_{ij} = \sum_k \beta_k X_{kij} + (\beta_h + \alpha_{y,p_i}) h_{ij} + \alpha_{y,m_i} + e_{y_{ij}} \text{ and } \ln(\sigma_{e_{y_{ij}}}^2) = \sum_l \gamma_l X_{lij} + \alpha_{y,v_i}$$

$$h_{ij} = \sum_n \beta_n X_{nij} + \alpha_{h_i} + e_{h_{ij}} \text{ and } \ln(\sigma_{e_{h_{ij}}}^2) = \sum_l \gamma_o X_{oij} + \alpha_{h,v_i}$$

Simulation structure

Simulations were conducted under a causal structure in which individuals first expressed habitat use, determined by a population-level intercept, individual-level variation in mean habitat preference, and individual-specific residual variance. Once habitat was assigned, trait expression was determined as a function of both individual baseline trait value and plasticity in response to the selected habitat. The slope of the trait–habitat relationship included both a population-level component and an individual-level deviation, allowing for among-individual variation in plasticity. Residual variation in trait expression also varied by individual. This generative process reflects a causal structure in which habitat influences trait expression, following the assumptions of the causal model. Parameter values used when generating the datasets are provided in Table 1. Data was generated for three scenarios varying by sample size and number of observations: 50 individuals with 10 observations each, 100 individuals with 5 observations each, and 100 individuals with 10 observations each.

The generative process involved specifying true parameter values for a continuous trait y and a continuous habitat feature h . Baseline values were defined, including the mean value of y ($y_{\text{intercept}}$), the mean value of h ($h_{\text{intercept}}$), plasticity of y as a function of h (y_h), and residual variance for both y (σ_y) and h (σ_h). Individual deviations from population-level parameters were simulated using a variance-covariance matrix constructed to capture relationships between traits and habitat features. This matrix was used to draw

samples from a multivariate normal distribution via the `MASS::mvrnorm()` function, allowing realistic variation among individuals.

Models were implemented using the `brms` package in R, which facilitates Bayesian inference. To improve computational efficiency, models were compiled with minimal iterations and saved as precompiled objects (.rds files) for subsequent updating. Each simulation run involved updating these precompiled models with a newly generated dataset using the `brms::update()` function. A total of three 300 simulation runs were performed per sampling scenario, with each run comprising 2000 iterations, distributed across two chains with a warmup period of 1000 iterations. The precompiled approach improved run time significantly. Since the time required to complete the model fitting process was lengthy, multiple R sessions were run simultaneously by adjusting the `model_range` variable, which was used when naming the output files.

Model outputs were saved and processed to extract estimates for both fixed and random effect parameters. These included population-level (fixed) effects and individual-level (random) effects. Summarized results for each model type were obtained by calculating means, standard deviations, standard errors and confidence intervals for all estimated parameters across the simulation runs.

All code used for this simulation study are publicly available on GitHub, ensuring full transparency and reproducibility of the analysis. (<https://github.com/Lamkhan/Habitat-as-a-trait>)

Statistical analysis

The evaluation of model performance was facilitated by the use of simulated data with known parameter values. This allowed for a straightforward comparison between model estimates and the true values specified during data generation. To assess the accuracy of each model,

we calculated the mean of the estimated parameters across 300 independent simulation runs and compared these to the corresponding true values.

Bias was assessed by determining whether each model consistently over or underestimated a given parameter across runs. Precision was evaluated by computing the standard error of the estimates across simulations. Additionally, 95% confidence intervals were generated for each averaged estimate, providing a measure of the uncertainty around the mean estimate for each parameter.

All models were evaluated using the same datasets to ensure comparability. Metrics were summarized separately for fixed effects and random effects allowing for a comprehensive assessment of both mean and variance components.

Results

Across all sample sizes and parameters, the causal model consistently produced unbiased estimates for the fixed effects. (Figures 1 - 5). In contrast, the univariate model systematically overestimated the plasticity in response to the habitat, parameter y_h (Figure 1). The univariate model also overestimated the intercept for the trait, parameter $y_{\text{intercept}}$ (Figure 2). The bivariate model was quite accurate in retrieving the intercept for the habitat feature (Figure 3) but greatly overestimated the intercept for the trait (Figure 2). The bivariate double hierarchical model was also accurate in estimating the intercept for the habitat feature (Figure 3), and overestimated the intercept for the trait (Figure 2). This model overestimated the residual variation in the habitat feature, parameter σ_h (Figure 4) and massively overestimated the residual variation in the trait, parameter σ_y (Figure 5). These trends were also seen in the random effects, the estimated standard deviations associated with each parameter, and correlations between each parameter. The causal model can estimate all the random effects with great accuracy where the other models fail to do so (Figures 6 – 10). The

bivariate model struggles particularly with estimating the among individual variance in mean habitat use, parameter $\text{sd}(\text{h_intercept})$ (figure 6) and the bivariate double hierarchical model when estimating the among individual variance in mean trait value, parameter $\text{sd}(\text{y_intercept})$ (figure 10). Overall, the standard errors associated with the estimates for each model were quite low (figure 11-20). For a fixed total number of observations, scenarios with more individuals and fewer repeated measures (e.g., 100 individuals with 5 observations each) outperformed those with fewer individuals and more repeated measures (e.g., 50 individuals with 10 observations each). This can be seen in Figures 2,3 and 4 where the sample structure with more individuals but less repeated observations have smaller confidence intervals, while maintaining a similar degree of accuracy. At realistic sample sizes between 500 and 1000, the causal model had sufficient data to accurately recover parameter estimates. Additionally, the causal model did not show evidence of overfitting, as it remained unbiased across all scenarios (Figures 1 – 10).

Discussion

This study evaluated the ability of different modeling approaches to recover individual variation and covariation in phenotypic plasticity and habitat use, using simulated data under controlled conditions. The results provide strong support for the causal structure mixed model as the most accurate and unbiased framework for estimating individual-level parameters, particularly in realistic ecological sampling scenarios.

The findings confirm the central hypothesis that causal models, which explicitly incorporate the directional relationship between phenotype and habitat, outperform traditional univariate and bivariate models in disentangling complex sources of variance associated to phenotypic plasticity and habitat choice. While univariate models consistently overestimated among-individual variation in plasticity (y_h), and all non-causal models inflated estimates of

the intercept for trait y ($y_{\text{intercept}}$), the causal model remained unbiased across nearly all conditions. Notably, at moderate sample sizes (500 - 1000 observations), the causal model was able to reliably estimate parameters without signs of overfitting. The univariate model is therefore not appropriate to use when studying populations, in which individuals vary in their available habitat and play an active role in selecting their habitat.

The overestimation of certain parameters by the univariate and bivariate models can be explained by the models being too simple to capture the trends/ground truths in the data that was generated. The univariate model does not at all consider the variation in habitat availability/selection whereas the bivariate models do not account for among-individual variation in plasticity. These are two assumptions which likely are not valid in many populations and certainly not valid given our simulated data. Since the bivariate models do not incorporate a random slope, they should not be used unless there is sufficient evidence to show that individuals in a population, respond in the same way to changes in habitat. It may be difficult to validate such an assumption and, in that case, it is safer to use the causal model. It is important to note that the data generated follows the causal mechanism in which it is assumed that individuals in the population vary in the habitat available, the habitat they actively select and how they respond to their habitat. One or more of these things may not be true depending on the natural population being studied. This is not necessarily a problem for the causal model because it can simply set those respective parameters to zero, if those sources of variation are not present in the natural population. There is, however, some risk of overfitting when one or more of these sources of variation are not present as the causal model is more complex than is required when studying those populations. For this reason, researchers should question, first is there some variation between individuals in the habitat they have available, do individuals vary in their ability/preference to select certain habitat

values and finally is there some causal link between the habitat selected and the phenotype at the individual level.

Traditional multivariate generalized linear mixed models can estimate covariation between traits and habitat use at different hierarchical levels, but they cannot quantify phenotypic plasticity directly or distinguish the direction of effects at the individual level. Likewise, while double-hierarchical generalized linear models offer improved sensitivity to individual differences in variance components, often interpreted as evidence for plasticity, they conflate true plastic responses with environmental variation or measurement error. By contrast, causal models offer a more nuanced and powerful framework, capable of partitioning variance and estimating directional plasticity, when data are appropriately structured.

Despite these strengths, causal models do come with limitations. They require complex model specifications and are computationally intensive, particularly for larger datasets or when extending to multiple traits or habitat features. Additionally, the accuracy of estimates depends on data being structured such that phenotype and habitat are measured concurrently and repeatedly across individuals. These models are also quite data hungry, missing data, or unbalanced sample sizes can particularly hurt the power of these models. While obtaining the necessary data was straightforward in simulation, it may be more challenging to achieve in empirical settings, particularly in natural populations.

This work contributes to a growing body of research that emphasizes the importance of individual variation in ecological and evolutionary processes. Understanding how traits covary with habitat use, through plasticity, habitat choice, or both, is essential for predicting how populations will respond to environmental change. The models tested here are especially relevant in the context of pace-of-life syndromes and behavioral ecology, where individual

differences in behavior or physiology are tightly linked to risk-taking, habitat selection, and fitness (Réale et al, 2010).

Future work should aim to extend these models to incorporate selection gradients by including fitness as an explicit outcome. This would allow testing whether trait-habitat combinations are adaptive and provide insights into the evolutionary dynamics of plasticity and habitat choice. Additionally, incorporating genetic pedigrees into causal models could enable estimation of additive genetic variance components, which are necessary for predicting evolutionary potential.

In conclusion, this study demonstrates the value of causal structure models for studying individual-level plasticity and habitat use. As habitat availability continues to change rapidly due to anthropogenic pressures, understanding how individuals adapt their traits and behaviors in response is critical. Simulation-based evaluations such as this provide a necessary foundation for applying these models in empirical systems and highlight the need for rich, repeated-measures datasets that can capture the complexity of trait-environment interactions in the wild.

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Table 1: True values for all parameters that were specified in the script for generating the datasets.

Parameter	Description	Value
y_intercept	Mean value of trait y (intercept)	0
y_h	Plasticity of trait y in response to habitat h (slope)	1
σ_y	Residual variance for trait y	0
Var(y_intercept)	Among-individual variance in mean trait y	0.3
Var(y_h)	Among-individual variance in plasticity (slope)	0.1
Var(σ_y)	Among-individual variance in residual variance of trait y	0.2
h_intercept	Mean value of habitat feature (intercept)	0
σ_h	Residual variance for habitat feature (within-individual variation in habitat use)	0
Var(h_intercept)	Among-individual variance in mean for habitat feature	0.3
Var(σ_h)	Among-individual variance in residual variance of habitat feature	0.2
All correlations	Correlation between all trait and habitat random effects	0.5

Figures

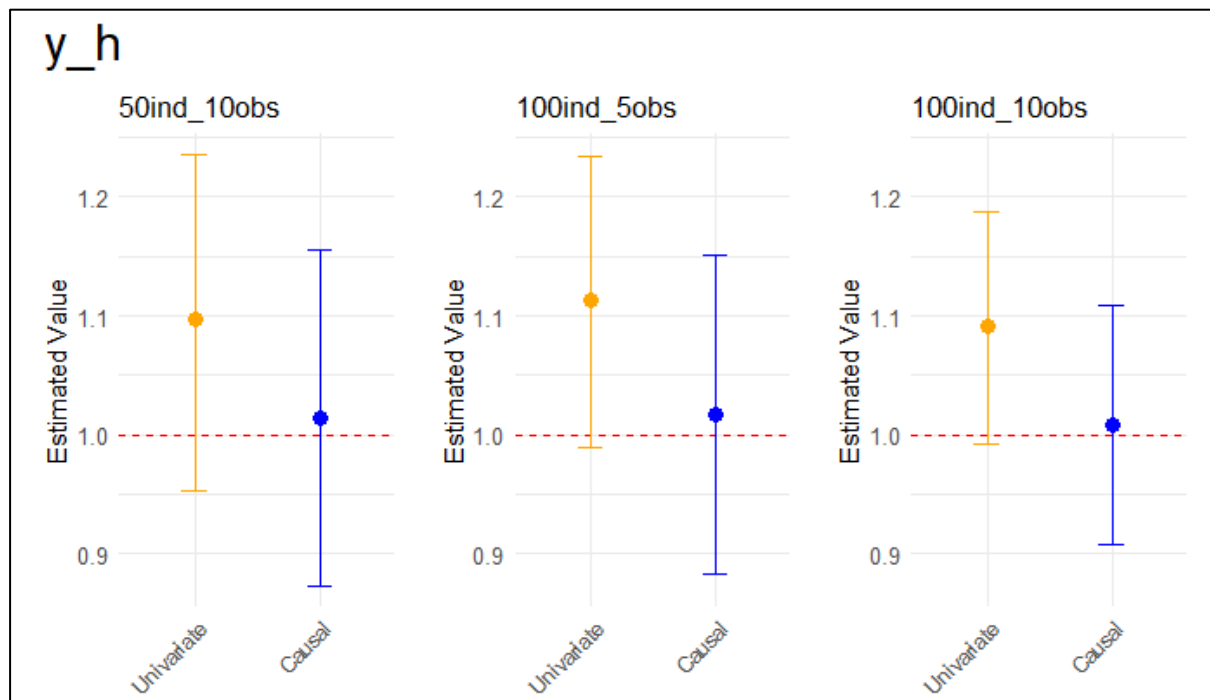


Figure 1: Average estimates of the parameter y_h (plasticity of the trait in response to habitat) across 300 simulation runs for each model. Estimates are shown for two model types: a univariate model (yellow) and a causal model (blue). Points indicate the mean estimated value of y_h , and error bars represent the 95% confidence intervals. The red dashed line denotes the true parameter value used in the simulations. This comparison illustrates differences in model performance and accuracy under varying data conditions.

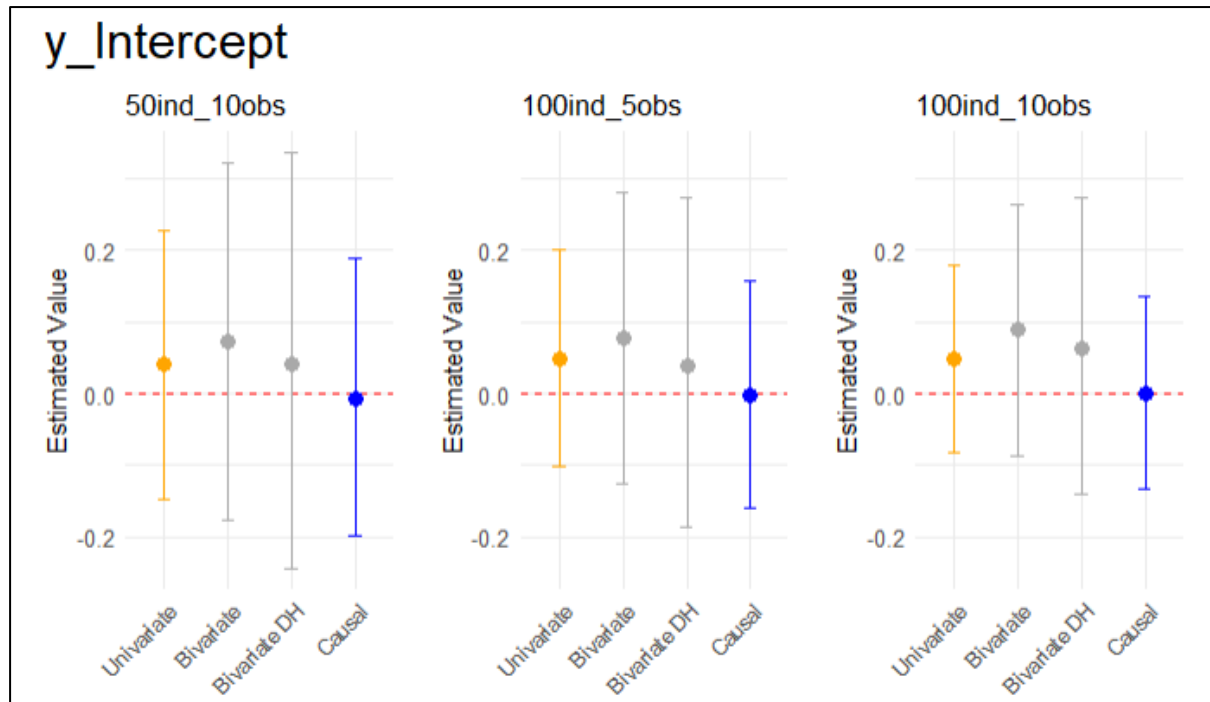


Figure 2: Average estimates of the parameter $y_intercept$ (baseline value of the phenotypic trait) across 300 simulation runs for each model. Estimates are shown for four model types: univariate, bivariate, bivariate double hierarchical (DH), and causal. Points represent the mean estimated value of $y_intercept$, with error bars indicating 95% confidence intervals. The red dashed line indicates the true parameter value specified in the simulations. This figure illustrates the accuracy and consistency of each model in estimating the trait intercept across varying data conditions.

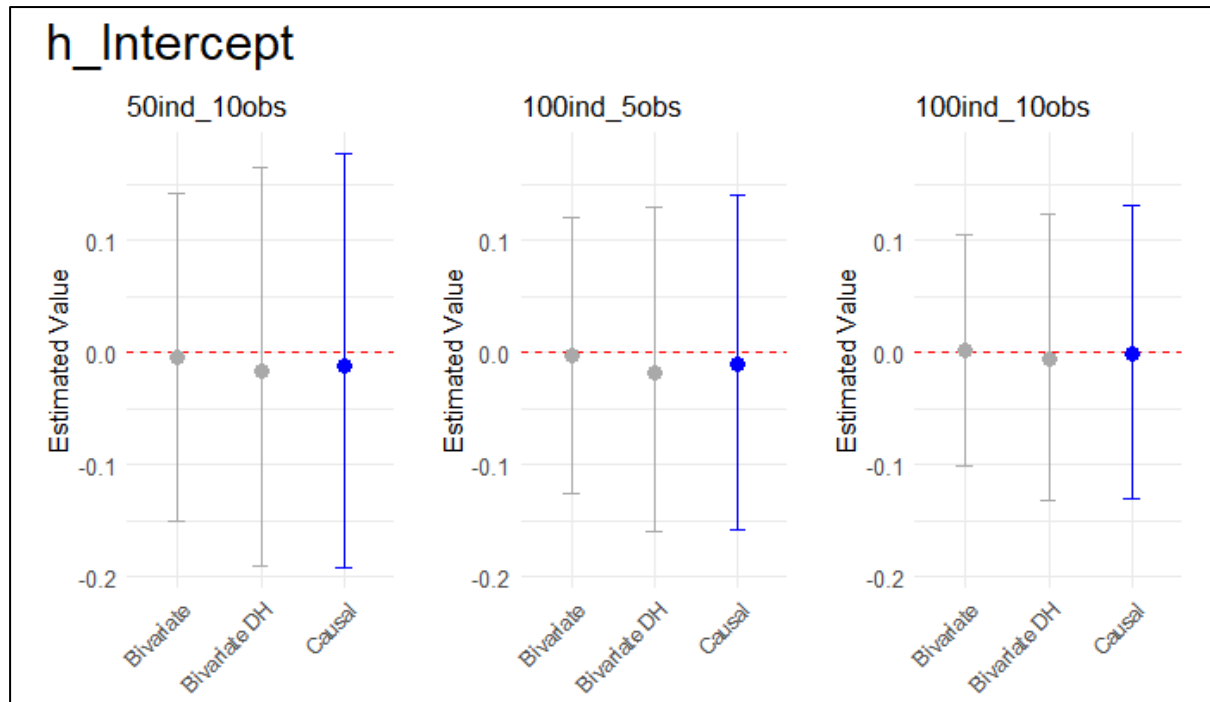


Figure 3: Average estimates of the parameter $h_intercept$ (baseline value of the habitat feature) across 300 simulation runs for each model. Estimates are shown for three model types: bivariate, bivariate double hierarchical (DH), and causal. Points represent the mean estimated value of $h_intercept$, with error bars indicating 95% confidence intervals. The red dashed line indicates the true parameter value specified in the simulations. This figure illustrates the accuracy of each model in recovering the baseline habitat value under varying data conditions.

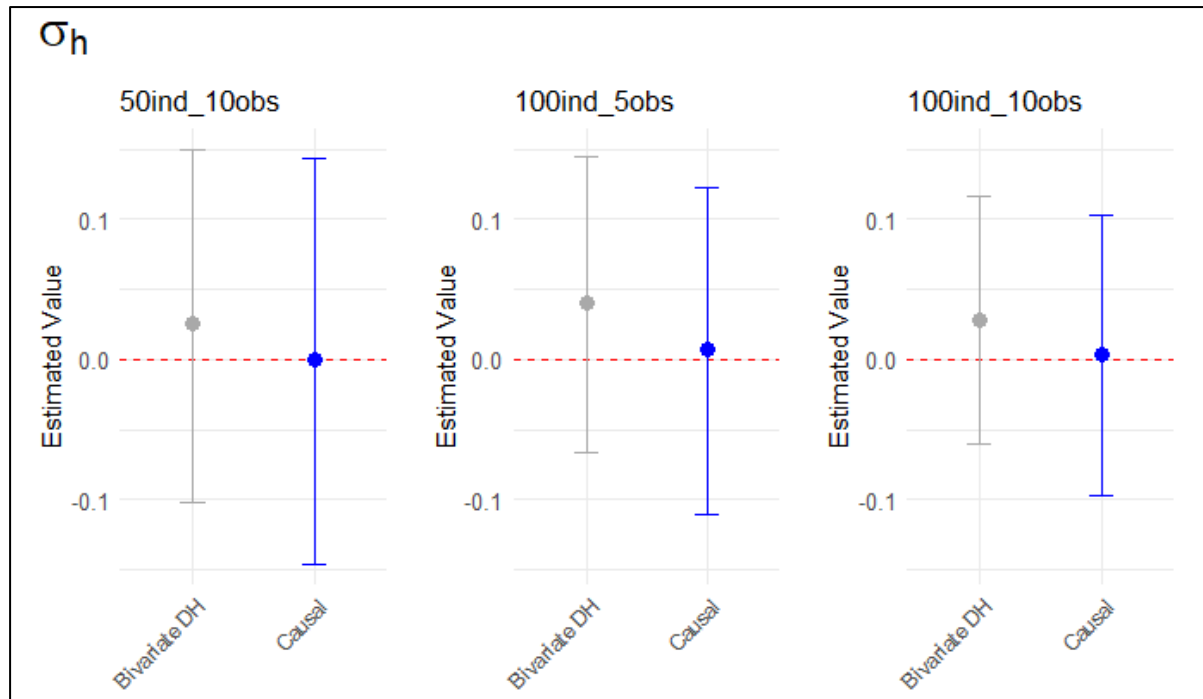


Figure 4: Average estimates of the parameter σ_h (residual variance of the habitat feature) across 300 simulation runs for each model. Estimates are shown for two model types: bivariate double hierarchical (DH) and causal. Points represent the mean estimated value of σ_h , with error bars indicating 95% confidence intervals. The red dashed line marks the true parameter value specified in the simulations. This figure evaluates how accurately each model recovers unexplained variation in habitat use.

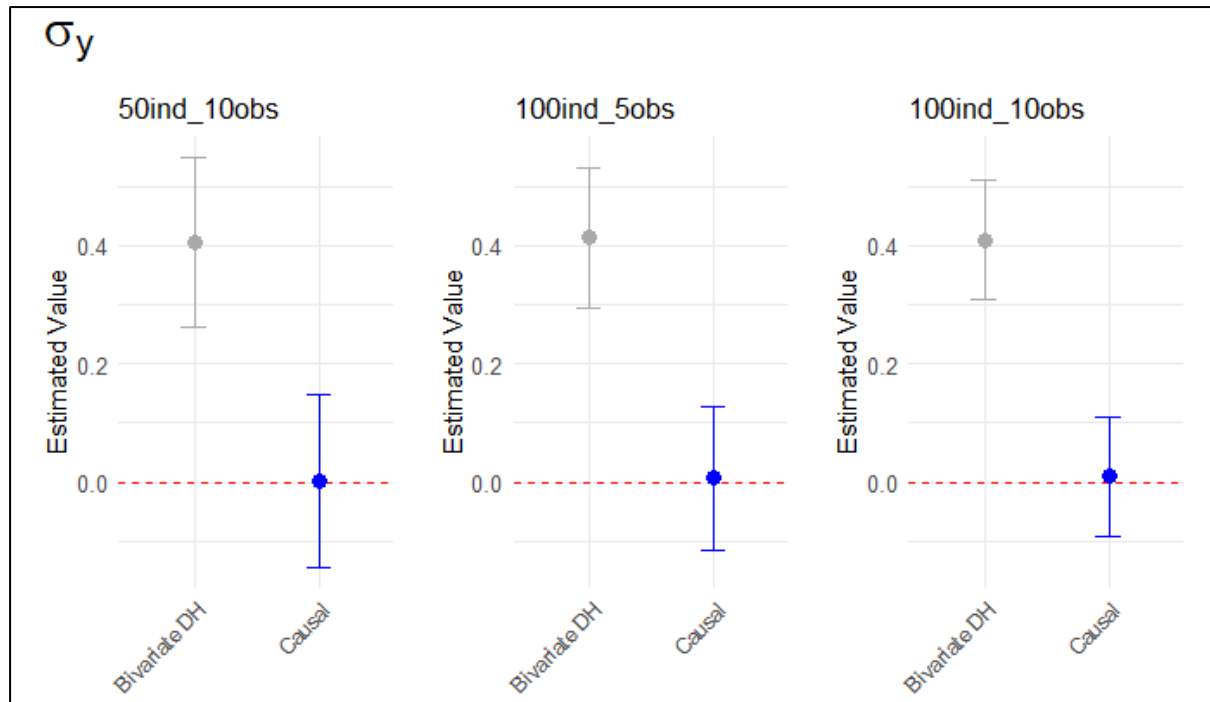


Figure 5: Average estimates of the parameter σ_y (residual variance of the trait) across 300 simulation runs for each model. Estimates are shown for two model types: bivariate double hierarchical (DH) and causal. Points represent the mean estimated value of σ_y , with error bars indicating 95% confidence intervals. The red dashed line marks the true parameter value specified in the simulations. This figure evaluates how accurately each model recovers unexplained variation in the phenotypic trait.

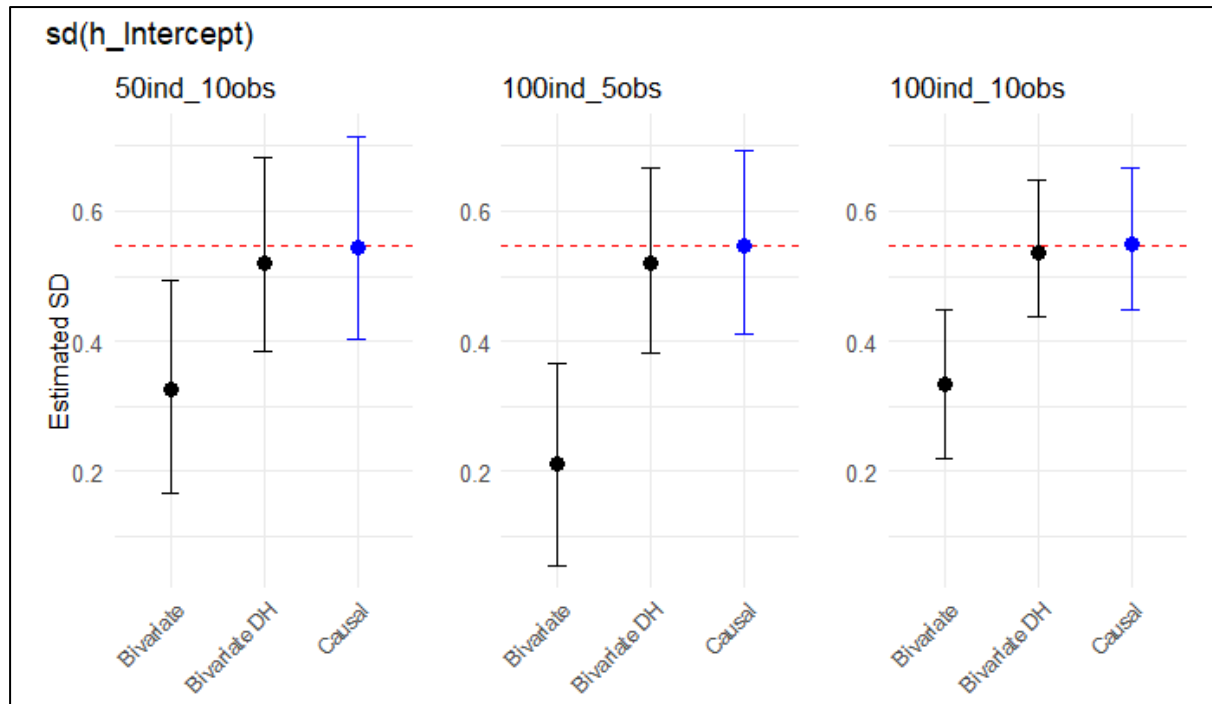


Figure 6: Average estimates of the standard deviation of $h_intercept$ (baseline value of the habitat feature) across 300 simulation runs for each model. Estimates are shown for three model types: bivariate, bivariate double hierarchical (DH), and causal. Points represent the mean estimated standard deviation, with error bars indicating 95% confidence intervals. The red dashed line marks the true parameter value specified in the simulations. This figure assesses each model's ability to recover variability in baseline habitat use across individuals.

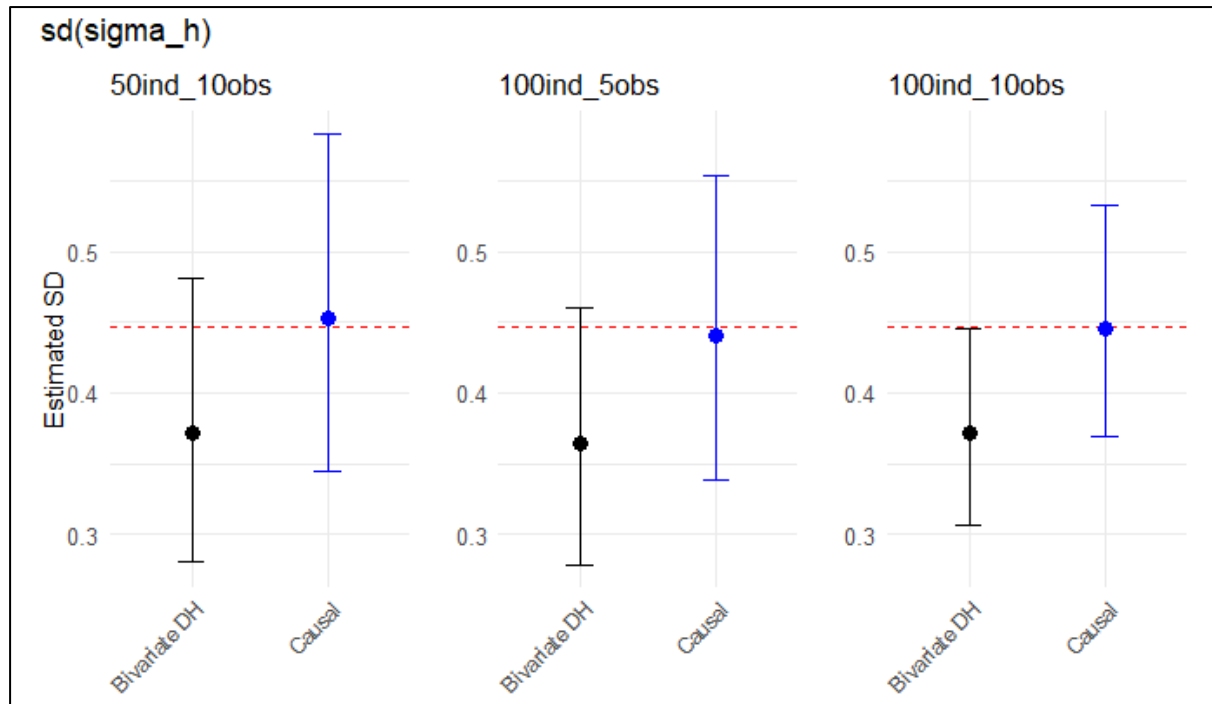


Figure 7: Average estimates of the standard deviation of σ_h (residual variance of the habitat feature) across 300 simulation runs for each model. Estimates are shown for two model types: bivariate double hierarchical (DH) and causal. Points represent the mean estimated standard deviation, with error bars indicating 95% confidence intervals. The red dashed line marks the true parameter value specified in the simulations. This figure assesses how accurately each model captures variability in unexplained habitat use.

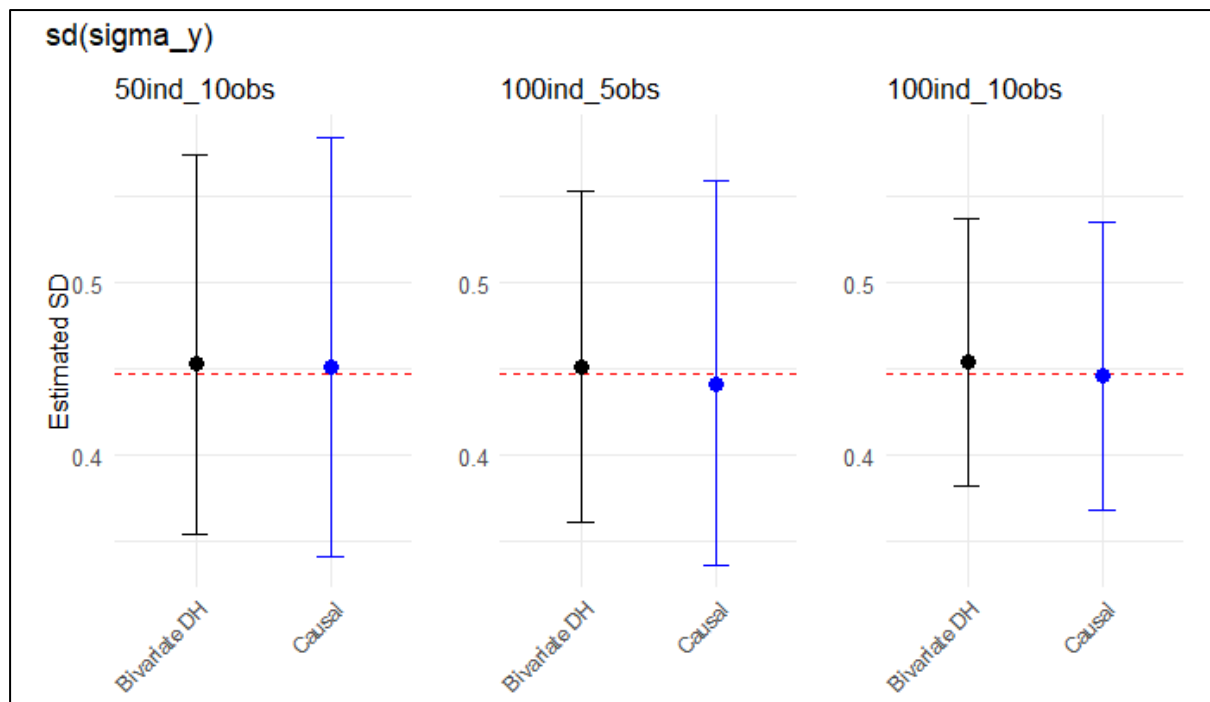


Figure 8: Average estimates of the standard deviation of σ_y (residual variance of the phenotypic trait) across 300 simulation runs for each model. Estimates are shown for two model types: bivariate double hierarchical (DH) and causal. Points represent the mean estimated standard deviation, with error bars indicating 95% confidence intervals. The red dashed line indicates the true parameter value specified in the simulations. This figure evaluates how well each model recovers variability in unexplained trait expression.

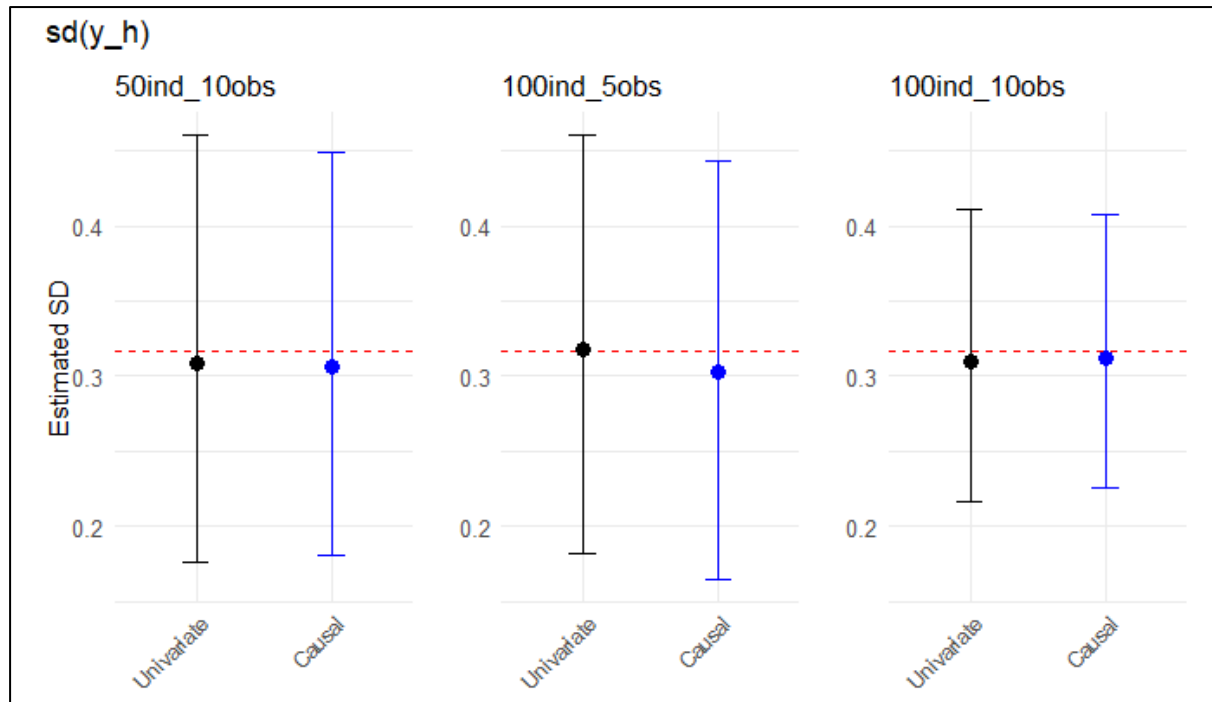


Figure 9: Average estimates of the standard deviation of y_h (plasticity in response to habitat) across 300 simulation runs for each model. Estimates are shown for two model types: univariate and causal. Points represent the mean estimated standard deviation, with error bars indicating 95% confidence intervals. The red dashed line indicates the true parameter value specified in the simulations. This figure evaluates how well each model recovers variability in plasticity.

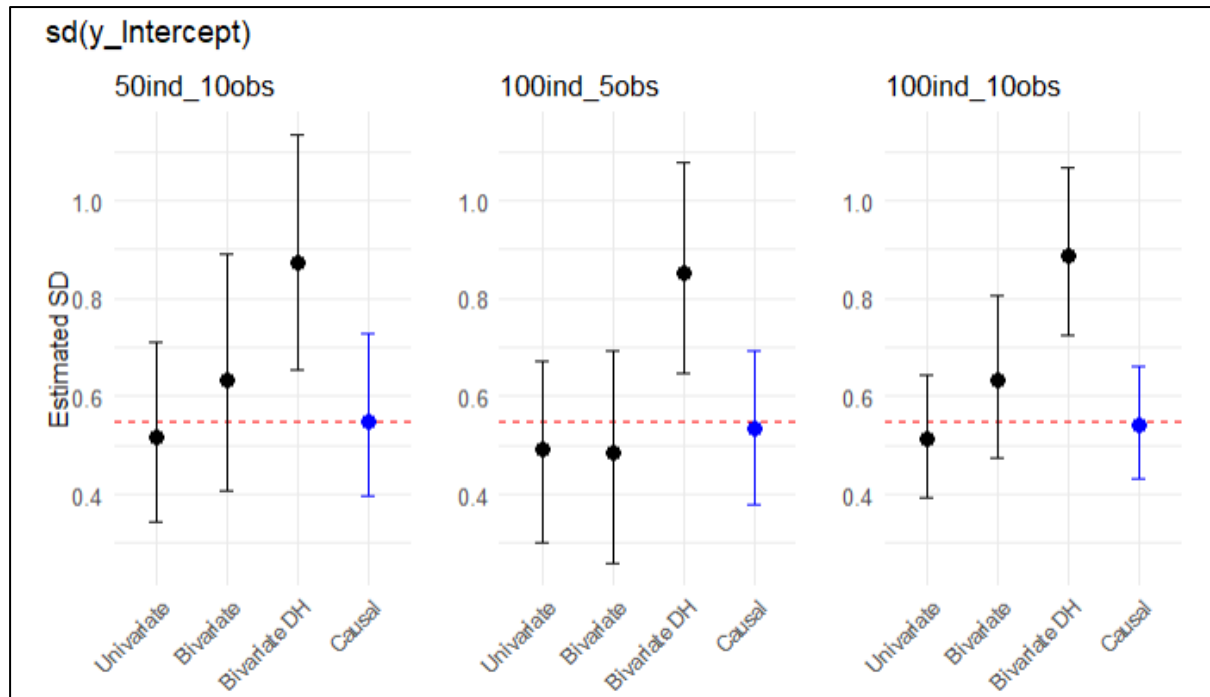


Figure 10: Average estimates of the standard deviation of $y_intercept$ (baseline value of trait) across 300 simulation runs for each model. Estimates are shown for four model types: univariate, bivariate, bivariate double hierarchical (DH) and causal. Points represent the mean estimated standard deviation, with error bars indicating 95% confidence intervals. The red dashed line indicates the true parameter value specified in the simulations. This figure evaluates how well each model recovers variability in trait intercept.

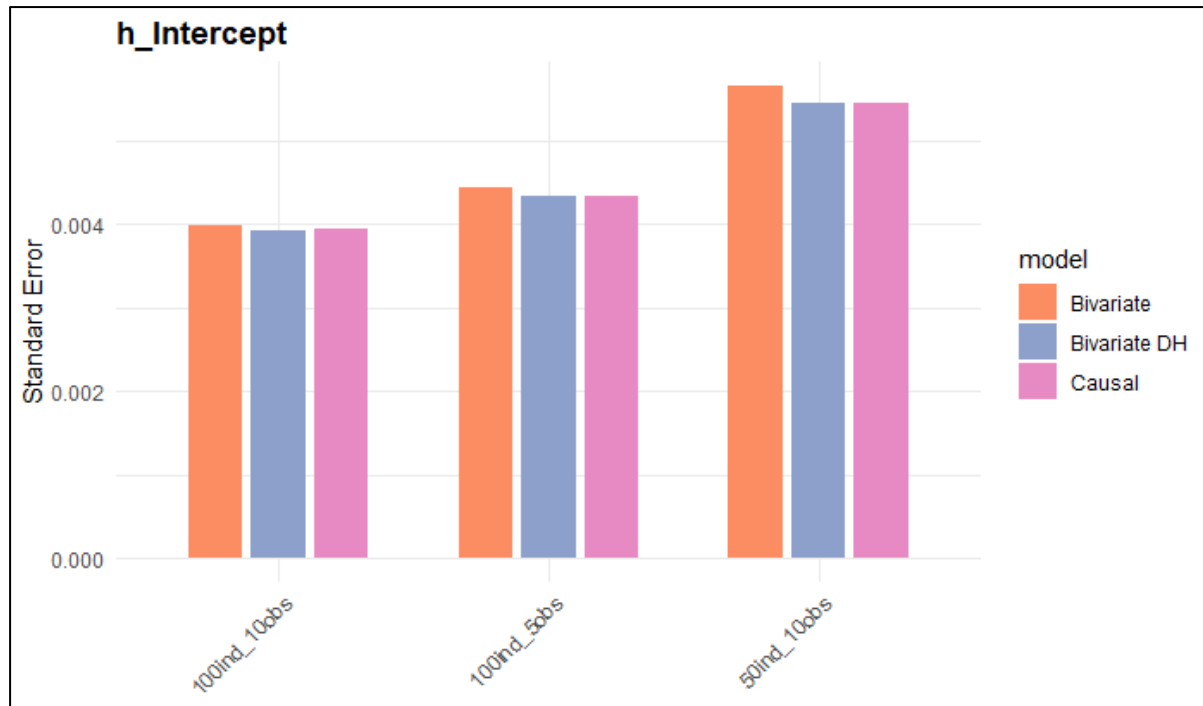


Figure 11: Standard error of the estimated mean habitat use ($h_{\text{intercept}}$) from each model.

Results are shown for three model types: bivariate, bivariate double hierarchical (DH), and causal, across different data scenarios. Bars represent the overall standard error of the parameter estimate, reflecting each model's precision in estimating the mean habitat value across the full simulation set. This figure illustrates how sampling design and model structure influence estimation certainty.

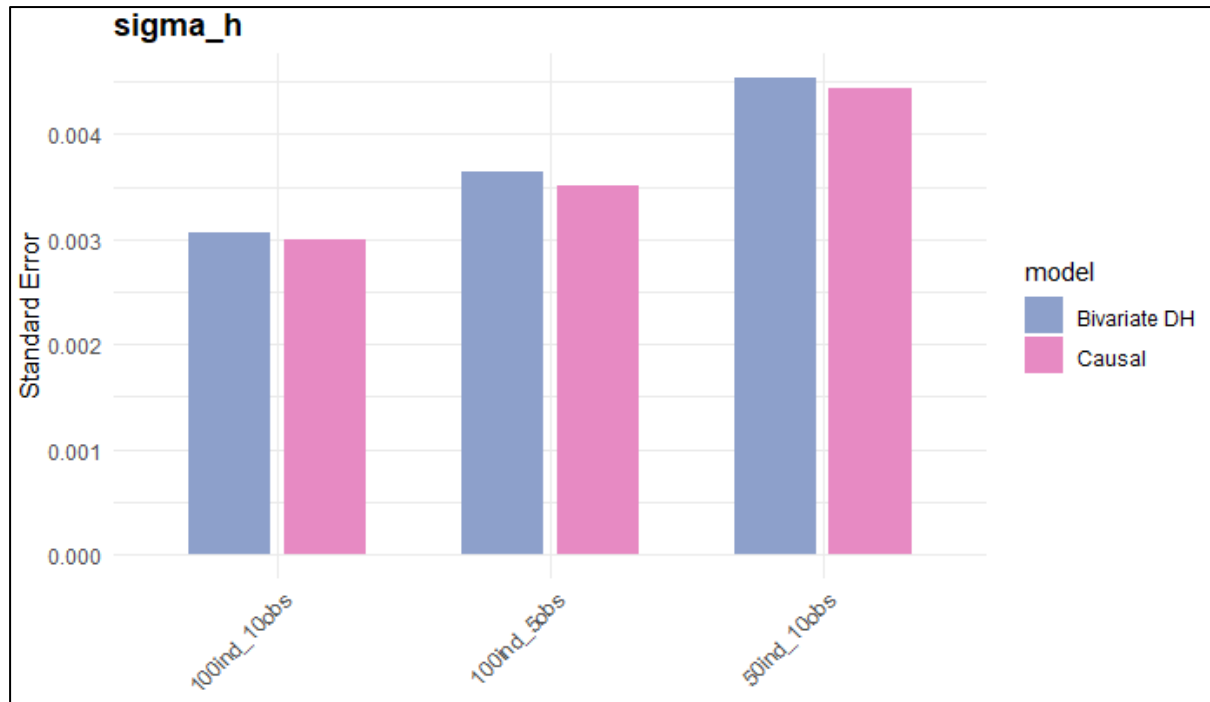


Figure 12: Standard error of the estimated residual variance in habitat use (σ_h) from each model. Results are shown for two model types: bivariate double hierarchical (DH) and causal, across different data scenarios. Bars represent the overall standard error of the parameter estimate, reflecting the precision of each model in estimating residual variance in habitat use. This figure highlights how model structure and sample design affect the certainty of variance estimation.

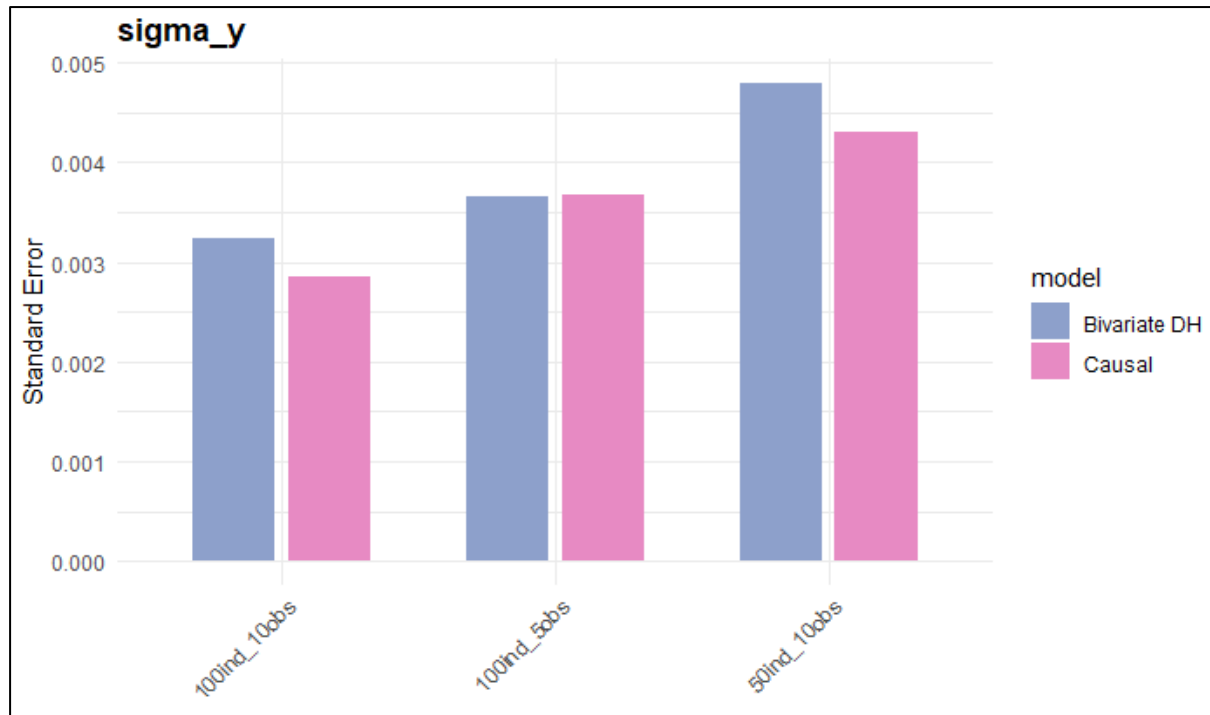


Figure 13: Standard error of the estimated residual variance in the phenotypic trait (σ_y) from each model. Results are shown for two model types: bivariate double hierarchical (DH) and causal, across different data scenarios. Bars represent the overall standard error of the parameter estimate, indicating each model's precision in estimating unexplained variation in trait expression.

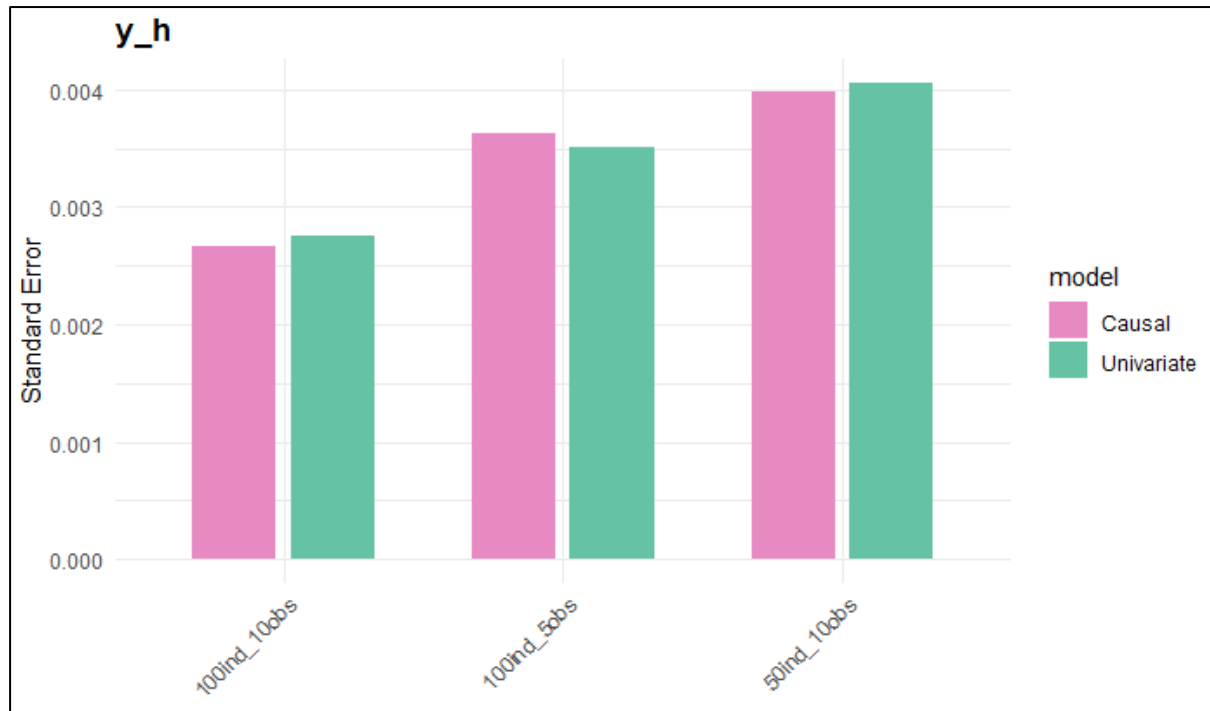


Figure 14: Standard error of the estimated plasticity of the trait in response to habitat (y_h) from each model. Results are shown for two model types: univariate and causal, across different data scenarios. Bars represent the overall standard error of the parameter estimate, reflecting each model's precision in estimating trait plasticity.

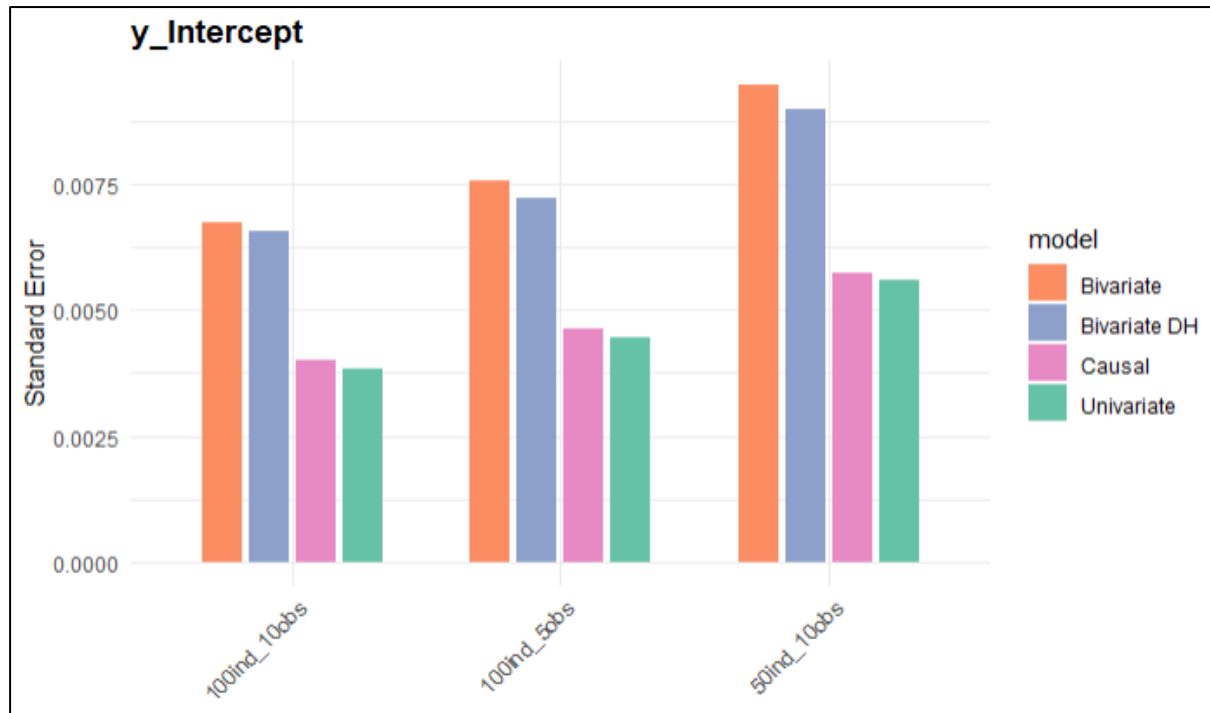


Figure 15: Standard error of the estimated mean trait value (y_intercept) from each model.

Results are shown for four model types: univariate, bivariate, bivariate double hierarchical (DH), and causal, across different data scenarios. Bars represent the overall standard error of the parameter estimate, reflecting each model's precision in estimating the baseline phenotypic trait value.

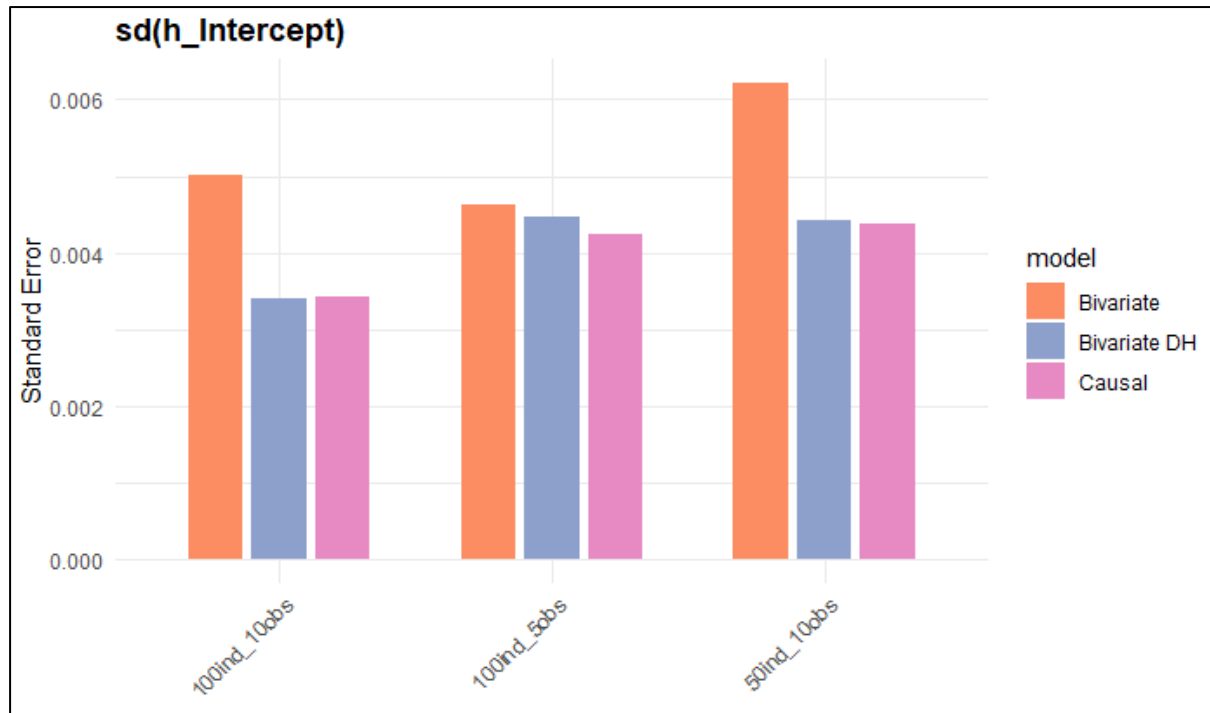


Figure 16: Standard error of the estimated standard deviation in the mean habitat use ($h_intercept$) from each model. Results are shown for three model types: bivariate, bivariate double hierarchical (DH), and causal, across different data scenarios. Bars represent the overall standard error of the estimated standard deviation, reflecting the precision of each model in capturing the baseline habitat feature value.

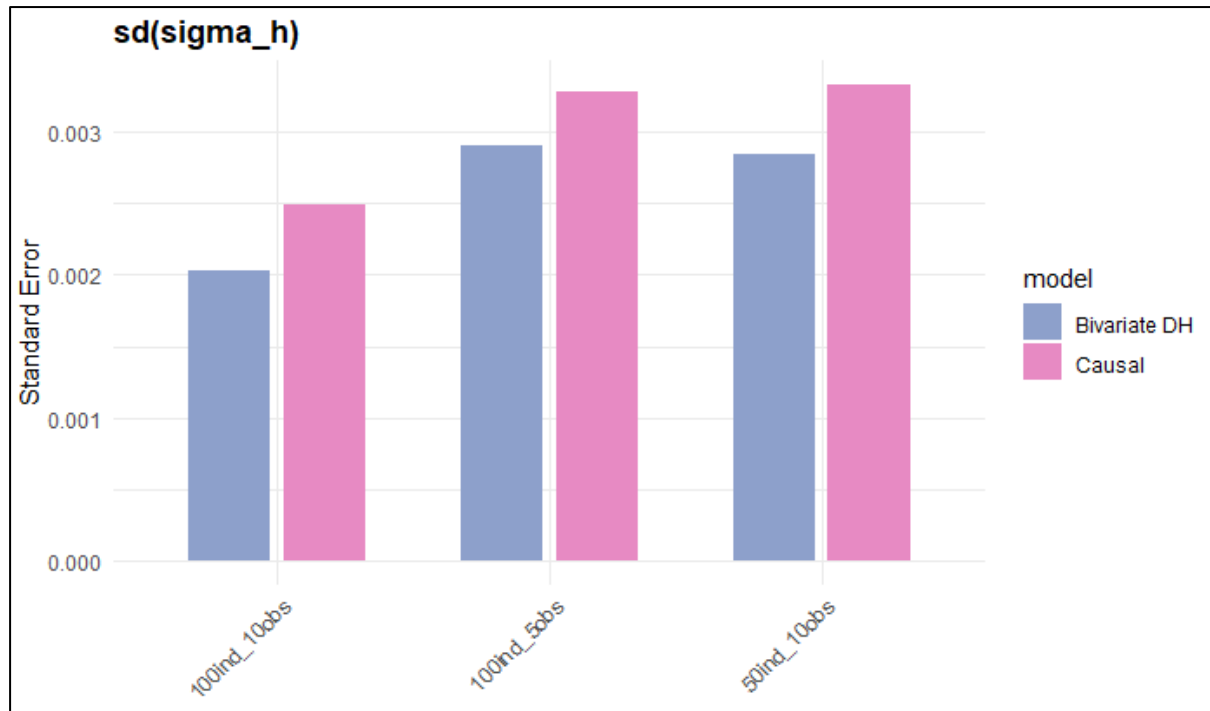


Figure 17: Standard error of the estimated standard deviation in residual variance of the habitat feature (σ_h) from each model. Results are shown for two model types: bivariate double hierarchical (DH) and causal, across different data scenarios. Bars represent the overall standard error of the estimated standard deviation, indicating the precision of each model in capturing variability in unexplained habitat use.

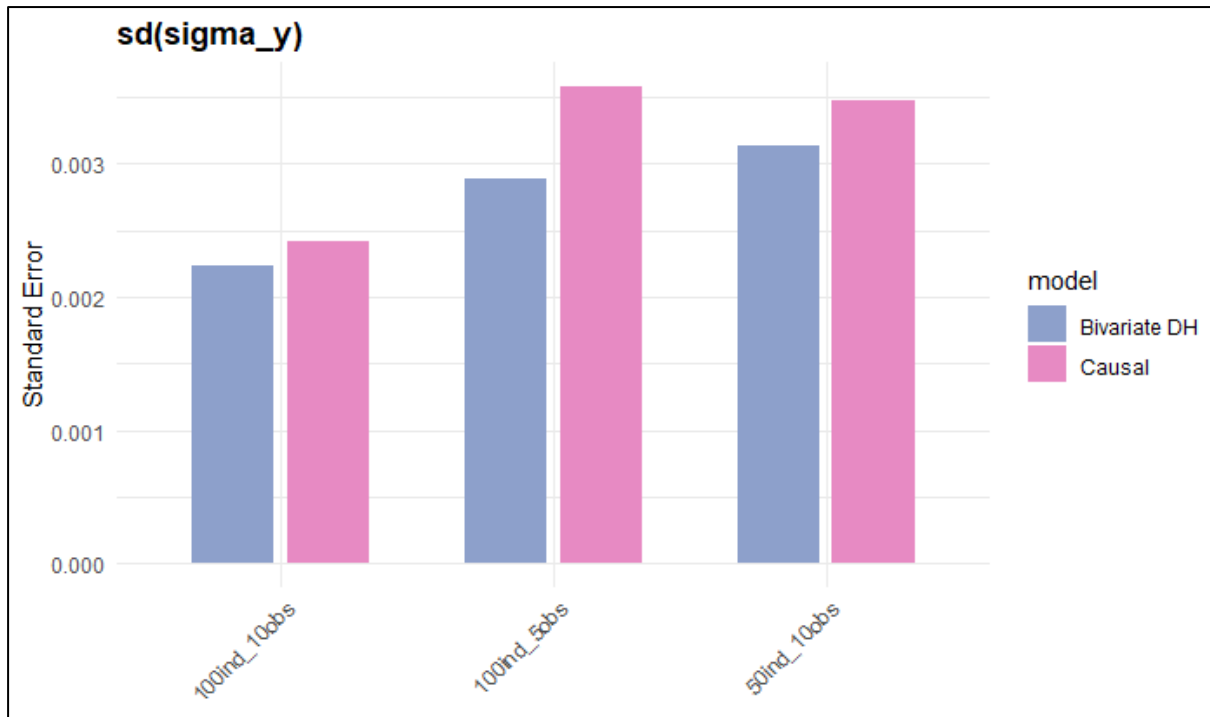


Figure 18: Standard error of the estimated standard deviation in residual variance of the phenotypic trait (σ_y) from each model. Results are shown for two model types: bivariate double hierarchical (DH) and causal, across different data scenarios. Bars represent the overall standard error of the estimated standard deviation, reflecting each model's precision in quantifying unexplained variation in trait expression.

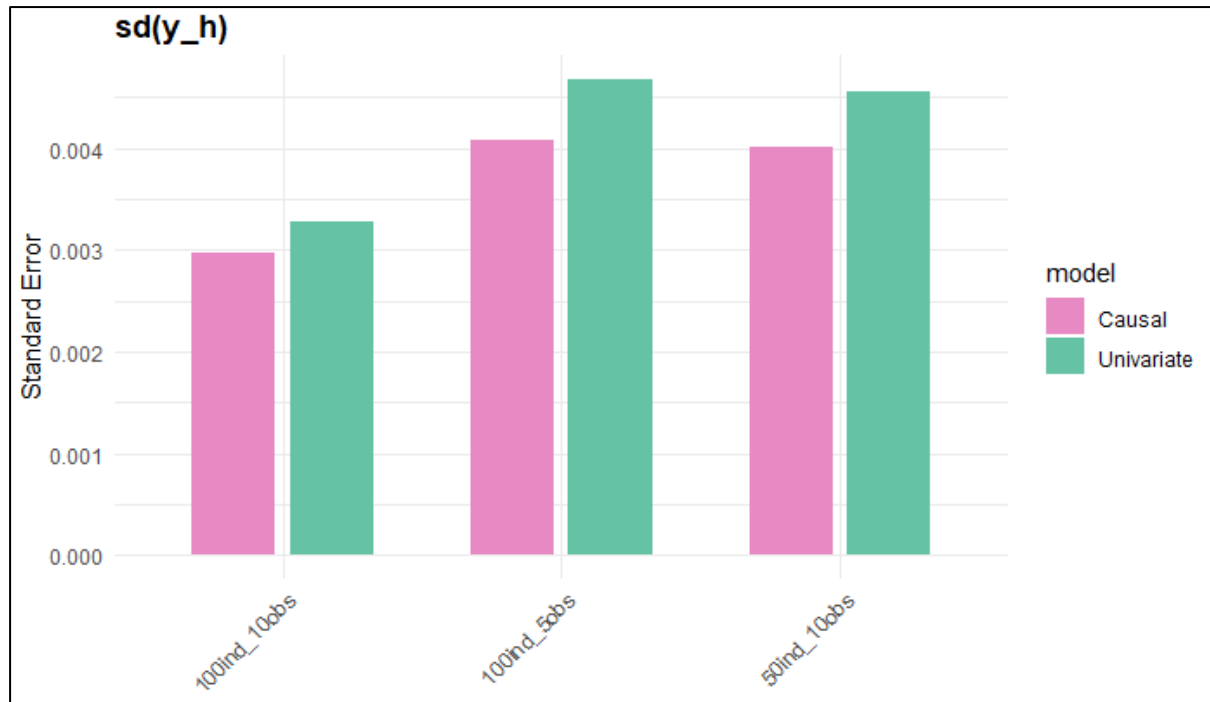


Figure 19: Standard error of the estimated standard deviation in plasticity of the trait in response to habitat (y_h) from each model. Results are shown for two model types: univariate and causal, across different data scenarios. Bars represent the overall standard error of the estimated standard deviation, indicating each model's precision in capturing variation in individual plasticity.

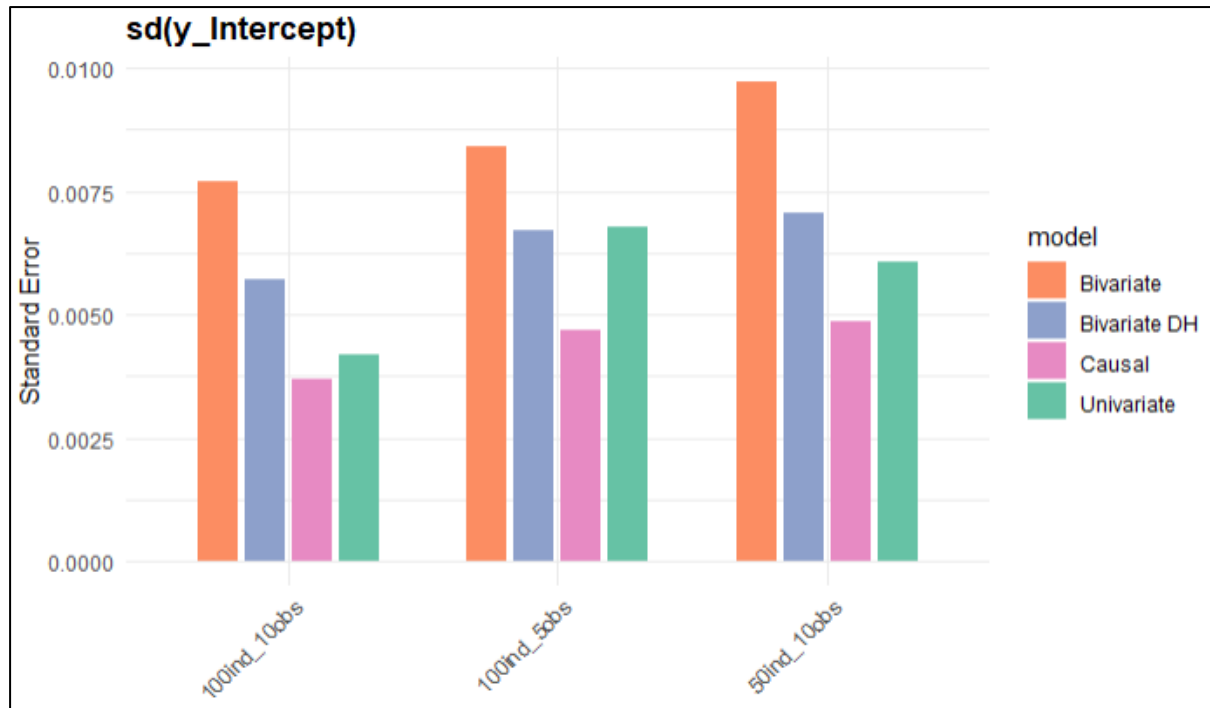


Figure 20: Standard error of the estimated standard deviation in mean trait value

(y_intercept) from each model. Results are shown for four model types: univariate, bivariate, bivariate double hierarchical (DH), and causal, across different data scenarios. Bars represent the overall standard error of the estimated standard deviation, indicating each model's precision in estimating variation in individual baseline trait expression.